Trade-offs between biodiversity conservation and maintaining fisheries yield from Australian marine environments; approaches using the Atlantis ecosystem modelling framework

by

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Declarations

Originality

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The following people contributed to the publication of the work undertaken as part of this thesis:

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Abstract

There is often a conflict between conservationists and the users of natural resources. This is just as much the case in marine management as it is on land. In order to practise ecosystem based fisheries management (EBFM), as mandated by law, we must address this conflict and find a system of management that protects both the ecosystems and those that exploit them for food production. This can only be done by increased understanding of the systems, both through empirical research and by developing tools, such as models that allow us to investigate trade-offs and alternative management strategies. Ecosystem models are becoming a popular tool for management strategy evaluation (MSE), as well as to explore ecosystem dynamics in the marine environment. This thesis examines aspects of the utility of the Atlantis ecosystem modelling framework, by:

- testing its ability to capture ecosystem dynamics in southern Australian waters, especially in and around marine protected areas, which are data rich areas;
- assessing the effects of alternative parameterisations and spatial structures within the model; and
- using it to assess possible impacts of various fishing management regimes.

Preliminary examinations in the first chapter of the thesis describe the results of simulations using a relatively simple model domain. The main findings of these examinations indicate that mesopelagic fish have the potential to form a critical link in south Australian ecosystems, possibly acting as a keystone species in the system. The ecosystem model is then further developed in subsequent chapters, with a new

modelling approach introduced for managing the spatial scale in models. A telescoping technique is explained that allows a large spatial domain to be modelled with a fine scale spatial structure where warranted and a coarse scale used to represent areas with fewer data available for parameterisation. This approach is an innovative extension of previous spatial resolution concepts that extends well beyond the range of scales previously considered. The implementation of this approach means the modelling framework is appropriate for exploring finely resolved spatial questions (e.g. around spatial management). This new capability is then used to test the results of the preliminary findings of the simple model, with additional model structures and parameterisations also compared to examine how the model structure may influence results. This examination reveals that spatial structure, as well as the way that trophic connectivity is parameterised, plays an important role in determining the importance of different species within the modelled ecosystem. The telescoping approach is also used to explore the further management issue of the effectiveness of no-take zones for providing increased yield outside of the protected area. This examination indicates that although no-take zones may help preserve biodiversity within the protected area, they are not sufficient to ensure sustainable fishing within the wider ecosystem context.

This thesis describes the benefits and appropriate utilisation of large, end-to-end ecosystem models, while also highlighting the limitations that must be acknowledged and taken into account. End-to-end ecosystem models cannot and should not be used as absolute predictors of ecosystem dynamics under perturbation. However, they are useful for informing on qualitative impacts that may arise from various ecosystem processes and uses. Furthermore, the work presented here demonstrates that the

parameter set chosen for a model will have significant impact on model output, highlighting the importance of empirical research to provide high quality data to furnish ecosystem models.

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Chapter 1. General introduction

Background to issue – ecosystem impacts of industrialised fishing

Loss of biodiversity, the collapse of fish stocks and the overall decline of the health of marine systems are well established issues (Pauly et al. 1998, Jackson et al. 2001, Myers & Worm 2003). The United Nations Food and Agriculture Organization notes that around 50% of the worlds wild fish stocks are over exploited (FAO 2010). Evidence suggests that ecological communities in the global oceans have been substantially changed through industrialised fishing; up to 90% of large predatory fishes have been lost since the 1950s, while the mean trophic level of both oceanic and inland catches declined in this time (Pauly et al. 1998). Changes in ecosystem structure and loss of biodiversity are a problem not only from a purely conservation perspective, they may also impact the ability of the oceans to provide ecosystem services such as maintenance of water quality, ecosystem stability and potential for stocks to recover from overfishing (Worm et al. 2006).

With the global human population potentially reaching 10 billion by 2100 (United Nations 2011) concerns are being raised regarding food security, especially in developing countries. Fisheries resources are an important source of protein and vitamins and micronutrient for many people, especially in rural areas of developing countries (Garcia & Rosenberg 2010). It has been estimated that between 15 and 20% of consumed animal protein comes from marine and inland fisheries (FAO 2010). An increasing population will put greater pressure on already stressed global fish stocks in order to produce enough high quality food. This predicament lends even greater

urgency to the need to understand the impacts of fishing on marine ecosystems so that they can be effectively managed for sustainable fishing.

Fisheries management, from MSY to EBFM

The increased pressures being put on marine resources, and the lags inherent in complex marine ecosystems, demand comprehensive and sophisticated management techniques from current fisheries managers, both for dealing with current problems but also as a means of forestalling future problems. The aims of fisheries management in the past has focused on maximising catch of a specific target species, whilst ignoring the impacts on predators, prey, habitat and other ecological interactions. The most commonly followed principle for fisheries management until the 1970 was Maximum Sustainable Yield (MSY). This concept was first introduced in the 1930, and gained increased popularity in the 1950s with the development of surplus-production models, which explicitly predicted MSY (e.g. (Schaefer 1954)). The inclusion of the concept of MSY in the 1982 United Nations Convention on the Law of the Sea meant that it gained status as a primary fisheries management goal. While it has been known for a long time that the total obtainable yield of a system is less than the sum of the individual species MSY (Larkin 1977, May et al. 1979), this concept is still ingrained in many approaches to fisheries management, albeit as a limit to be avoided rather than a goal to be reached (Mace 2001). There have been many criticisms of the MSY approach in more recent years (summarised in Punt and Smith (2001)). Two relevant criticisms of individual species stock assessments are: firstly the health of the entire ecosystem is not considered; and secondly, target species interact with their ecosystem in complex ways, and by not taking those interactions into account, one risks misunderstanding the dynamics and available stocks of the target species in question. Indeed, the current state of fisheries around the world

demonstrates that the MSY has not been sufficient to manage fisheries without continued declining stocks and profits.

These unanticipated ecosystem consequences of fishing are becoming increasingly recognised and have prompted the move away from the single species approach and towards Ecosystem Based Fishery Management or EBFM (Pikitch et al. 2004). EBFM aims to change the priority of fisheries management, from maximising catch to focus on the ecosystem as a whole. The intention of this is not only conservation, but also to move towards more sustainable fishing, where reasonable yields of target species can be maintained for the long term without compromising the surrounding and supporting system structure. A definition of EBFM, agreed to by over 200 academic scientists from institutions in the USA, is:

> Ecosystem-based management is an integrated approach to management that considers the entire ecosystem, including humans. The goal of ecosystem-based management is to maintain an ecosystem in a healthy, productive and resilient condition so that it can provide the services humans want and need. Ecosystem-based management differs from current approaches that usually focus on a single species, sector, activity or concern; it considers the cumulative impacts of different sectors.
> (McLeod et al. 2005)

EBFM has recently been introduced into legislation in many countries, requiring that fisheries demonstrate that they are not having a negative impact on the wider ecosystem. Obtaining a better understanding of the impacts of fishing on the trophic structure of ecosystems is therefore paramount to being able to meet this legal requirement.

Although EBFM is widely agreed upon in principle, it can be difficult to employ in practise. The vast scale and complexity of ecosystem dynamics, including the breadth of species and impacts that may occur in ecosystems, means that gaining a

comprehensive understand of the entire system is an immense, if not impossible undertaking. For example, indirect effects of fishing have caused trophic cascades and in some cases complete regime shifts in many marine systems (Frank et al. 2005, Daskalov et al. 2007, Andersen & Pedersen 2009). The causes of these changes can be varied and complex; based on either anthropogenic factors such as overfishing, pollution, climate change and introduction of invasive species, or by internal perturbations within the system, or indeed, a combination of these (Daskalov et al. 2007). Exploring the causes of these cascades in real ecosystems is difficult without a comprehensive understanding of the dynamics of the system in question.

The use of ecosystem models to improve our understanding of marine ecosystems and as fisheries management tools

Ecosystem models are becoming a more widely used tool to facilitate the exploration of multiple management strategies on the marine environment. These models are a tool that can provide a greater insight into the complex relationships between habitat structure, species composition, food webs and multiple uses of marine ecosystems. The term ‘ecosystem model’ can refer to a large range of model types from ones covering just a few higher trophic level groups (e.g. suites of target species in fisheries models), or those that focus on the ‘bottom’ end of the food web (e.g. plankton groups in water quality models). For the purposes of the work presented in this thesis, the term ‘ecosystem model’ will be used to describe a model that represents the entire food web. While there have been a number of entire trophic marine ecosystem models (for example Ecopath with Ecosim (EwE) (Christensen & Pauly 1992), ERSEM I (Baretta et al. 1995) and OSMOSE (Shin & Cury 2001)), whose use is increasing rapidly (Fulton 2010), in comparison to the use of fisheries or water quality models, the use of these ecosystem models is still limited.

The development and use of ecosystem models for fisheries management is important if we are to quantify the impact of management strategies. Furthermore, in order to investigate EBFM scenarios, ecosystem models not only must be multi-species, they must also be spatially explicit to be able to capture movement dynamics of biological components of the system. However, this extra requirement raises its own issues, such as increased data requirements for parameterisation and calibration, increased computational power requirements and the increased complexity of model output, which makes producing and using highly spatially-resolved models difficult (Fulton et al. 2003). As a result, ecosystem models in the past have often been built with either no spatial resolution (Walters et al. 1997, Bissett et al. 1999, Cury et al. 2000) or with large areas represented by relatively few boxes. (Baretta et al. 1995, Fulton & Smith 2004).

Although these models have gained popularity over the past few decades, further work is required to develop and refine their use. Ecosystem models explicitly represent complex trophic webs, nutrient dynamics, temporal variation and forcing. Implementation of these models requires addressing challenges such as the choice of model structure, temporal and spatial scaling and biological structure, such as the compartmentalisation of functional groups. Ecosystems models may be sensitive to all of these choices, and therefore require ecological knowledge and rigorous application to utilise them properly (Allen 2010). Indeed, issues remain as to how complex ecosystem models need to be to be able to represent relevant dynamics, but still remain computationally and analytically tractable. Furthermore, ecosystem models require vastly more data inputs than do single species models, which results in an increase in both the time and cost required to develop them. These sophisticated

models bridge the gap between fisheries and water quality models, but are still in a relatively new state compared with other traditional fisheries management tools.

An important role of ecosystem models is to allow the controlled exploration of a complex system and to identify gaps in our understanding of marine systems (Lozano-Montes et al. 2011). Models provide a test-bed to investigate how various ecosystem dynamics can play out under perturbation scenarios. There is currently significant uncertainty in our knowledge of assumed system states and properties of marine systems. This thesis uses models to explore marine system states under two topical management regimes in order to further our understanding of marine ecosystem dynamics. These management issues are; the use of marine protected areas (MPAs) to achieve EBFM and the ecosystem impacts of fishing on lower trophic level species. The particular issues surrounding these topics and the need for further understanding of their impacts on marine ecosystems, are provided below.

The use of Marine Protected Areas to achieve EBFM

EBFM requires that potential cumulative effects of multiple uses of the marine system are addressed rather than the traditional sector by sector approach. This is especially important in areas where there may be conflicts between users and the environment, and can be achieved through the integrated management of multiple sectors. During the past 10-15 years, marine spatial planning has become a crucial tool for integrating management of multiple uses and moving towards EBFM (Douvere & Ehler 2008). One of the best-known examples of such management is the Great Barrier Reef Marine Park (GBRMP), where human activities such as fisheries and tourism occur, while simultaneously providing a high level of protection for specific areas. Fisheries management using MPAs is, however, non-traditional, and as such can be

controversial (Hart & Sissenwine 2009). There is therefore a strong need to ensure that MPAs will in fact provide a benefit.

Research on MPAs to date has shown that the benefits and impacts of this form of management differ depending on size and type of MPA, other concurrent management practises or on the individual system dynamics (Halpern et al. 2004, Baskett 2006, Buxton et al. 2006, Hilborn et al. 2006, Andersen & Pedersen 2009). For example, although some species have been shown to benefit from the protection from fishing inside MPAs (e.g lobsters in Tasmanian MPAs (Edgar & Barrett 1999), trophically mediated indirect effects of protection may cause the opposite effect for other (e.g. prey) species, and potentially a loss of biodiversity for the system as a whole (Savina et al. 2009). As recent work has shown, the biodiversity benefits of MPAs are dependent on the surrounding context (Eklof et al. 2009, Kaplan et al. 2010). It is therefore imperative that further work be done to understand the ecosystem dynamics that influence the success or otherwise of MPAs. Although empirical data collection both inside and outside of an MPA allows us to assess the relative biology in both regions, it does not explain why these differences occur. Moreover, empirical data is often difficult and time consuming to acquire in regards to the biological impacts of MPAs, making it problematic to assess whether the closures are indeed meeting the conservation and fisheries goals.

Ecosystem impacts of fishing lower trophic level species

Ecosystem impacts at lower trophic levels have been observed from the reduction in higher trophic level species, due to cascade effects down through the food web to the lower levels (Myers & Worm 2003, Estes et al. 2011). In contrast, trophic cascades or regime shifts caused by overfishing of species lower in the food web have been less well studied, mainly because of the historically lower incidence of fishing on these

groups. This however is changing, as lower trophic level species now account for over 30% of global fish landings (Alder et al. 2008). The increase in landings of lower trophic level species is of particular concern, as the potential ecosystem consequences are unknown. Lower trophic level species may play a crucial role in marine food webs, transferring production from primary producer to higher trophic level species (Smith et al. 2011). Increased catches of krill in the Southern Ocean, for example, are of concern due to the potential to impact on the recovery of depleted marine mammals such as whales, which rely on krill as a major food source (Constable et al. 2000). Lower trophic level species contribute directly to food security in many developing countries, with 10 to 20% of global landings being consumed directly by humans (Tacon & Metian 2009). Although aquaculture production is one alternative that is increasingly used as a means to supplement the supply of wild caught fish, this is not a simple solution, as it also has biodiversity and conservation consequences, including potential impacts on wild fish stocks (Diana 2009). One particularly pressing concern is that fishmeal for aquaculture feed is often produced from wild caught lower trophic level fish, which are already under pressure for human food security. Because of increases in global demand for fertiliser, animal feed and increases in the production of seafood from aquaculture, demand for fishmeal continues to increase (Merino et al. 2008) Understanding the impacts of fishing on these lower trophic levels is essential if we are to maintain EBFM principles.

Research objective and thesis outline

The basis for this research was the general need for critical exploration of the ecosystem dynamics affected by the two marine management issues outlined above; the use of marine protected areas to achieve EBFM and the ecosystem impacts of fishing on lower trophic level species. However, the objectives also encompass

broader issues of model development and structure. This work will contribute to a better understanding of how ecosystem models can contribute to ecosystem understanding and fisheries management, as well as the limitations of model applicability. This is achieved through the implementation of multiple Atlantis models that cover variations in model spatial and biological parameterisation.

The outline of the thesis is as follows:

Chapter 2. Ecosystem impacts of high fishing mortality on squid and myctophid stocks in south-eastern Tasmania

The chapter introduces a spatially simple Atlantis model, which is used to investigate the ecological impact of increased fishing pressure on the lower trophic groups located off south-eastern Tasmania. In particular, scenarios of high-level fishing pressure on both squid and fish from the family Myctophidae are examined.

Chapter 3. The use of telescoping spatial scales to capture inshore to slope dynamics in marine ecosystem modelling

This chapter builds on the smaller model developed in chapter one, to produce a more spatially complex model that covers a larger spatial domain. The model covers the waters off south-eastern Australia and uses a polygonal telescoping approach, which incorporates fine-scale detail in the coastal zone, increasing in scale to a very coarse scale in offshore waters. The fine-scale resolution of the reef and coastal areas reproduces observed trends in reef fish abundances. This telescoping technique is a useful tool for incorporating a wide range of habitats at different scales into a single model.

Chapter 4. Implications of model parameterisation and spatial structure when assessing the ecosystem impacts of a reduction in pelagic forage species

This chapter replicates the examination conducted in chapter 2, but with alternative model domains that have been developed through chapters 2 and 3, along with additional Atlantis models that were developed for previous work. Chapter 4 explores whether the results obtained from a spatially simple model can be replicated using models with a more complex spatial domain. The work presented here forms the basis of my contribution to a paper recently published in Science (Smith et al. 2011).

Chapter 5. Using a telescoping approach to model ecosystem impacts of the implementation of Marine Protected Areas

This chapter takes the telescoping approach introduced in chapter 3 and applies it to a topical management issue in fisheries: the impact that marine protected areas (MPAs) have on marine ecosystems. One of the main factors that influences how effective an MPA is in a modelled ecosystems is the level of movement of organisms, both in the larval stages and as adults. When using modelled systems to exploring the effectiveness of MPAs it is therefore imperative to give consideration to the movement of the biotic components and the spatial structure of the model through which these components can move. The telescoping approach is an appropriate method to model fine scale spatial structure around the closed areas, to provide a more detailed representation of fish movement and therefore the effects of the introduction of the MPA.

Chapter 6. General discussion and conclusions

This chapter provides a summary of the main finding and discusses the implications of the work presented here and the relevance to fisheries management and the understanding of marine ecosystems.

Thesis structure

Excluding this introductory chapter (Chapter 1) and the final discussion chapter (Chapter 6) this thesis has been written as a series of separate scientific research articles. Chapter 3 has been published in Natural Resource Modeling and Chapters 2 and 5 are currently in internal review at CSIRO. Chapter 4 formed the basis of a contribution to a larger collaborative work, which was recently published in Science (however chapter 4 in the form presented here has not been submitted for publication). As these chapters have been written as stand alone papers, there may be some repetition in content, particularly in the Introduction and Methods sections, in order to meet journal requirements. In each of these chapters I was the senior author, responsible for model development, data interpretation and analysis and the writing of the manuscript. My co-authors contributed to provision of input data for the model and to preparation and critical review of manuscripts for publication. The co-authors' contribution is detailed in the statement of publication and co-authorship.

Chapter 2. Ecosystem impacts of high fishing mortality on squid and myctophid stocks in south-eastern Tasmania

Abstract

The wider ecological impacts of fishing are often difficult to predict, making ecologically sustainable fisheries management problematic. Ecosystem models have been developed as tools that can assist in ecosystem management and system level understanding. In this chapter, the Atlantis framework is utilised to create an ecosystem model to investigate the ecological impact of increased fishing pressure on the lower trophic groups located off south-eastern Tasmania. Scenarios of high level fishing pressure on both squid and fish from the family Myctophidae were examined. This ecosystem was found to be robust to high levels of fishing on squid populations, however, high levels of fishing on myctophids caused greater ecosystem impacts.

Introduction

The concept of ecologically sustainable development has grown globally in recent years, so that the wider ecological impacts of fisheries on marine ecosystems must now be incorporated into fisheries management (Sainsbury & Sumaila 2003). The ecological impacts of fishing have prompted legislation that requires fisheries management to take into account ecosystem impacts, not merely sustainable fishing of target species. While historically the impact of fishing on target species has seen much research, the corresponding impact on habitats or ecosystem function within these ecosystems is a more recent and less well understood area of study. Recent reviews of the ecological effects of fishing show that fishing can cause strong indirect ecological impacts (Goñi 1998, Hall 1999, Pauly et al. 2003). Cascading effects through trophic webs are difficult to predict, and the unforseen consequences that can arise from fishing include: the restructuring of trophic linkages; predation or competition release from the removal of target species; changes to the demographic structure of either target or non-target species (eg, sex, size or age ratio changes); and a loss of genetic diversity or change in genetic frequency in target and non-target species. Changes in demographic and genetic structure typically lead to shifts in age and size of maturity, fecundity and potentially natural mortality.

Effective management tools and strategies must be established to ensure a sustainable food resource in the oceans. Ecosystem models have been developed as tools that can assist in ecosystem management and system level understanding. End-to-end (whole-of-ecosystem) models incorporate both higher and lower trophic levels as well as nutrient cycling, hydrodynamic and fisheries components. They therefore allow more comprehensive investigations into the functioning of marine ecosystems under various

environmental conditions or fisheries management regimes. They also provide insight into the linkages and processes that occur in both natural and perturbed marine systems, beyond that which can be gained from studying a single species or impact.

The global trend in world fisheries is that we are fishing both down (Pauly et al. 1998) and through (Essington et al. 2006) the food web. As fisheries remove the larger piscivores, increasing fishing effort is being put on all parts of the ecosystem (Branch et al. 2010) including invertebrates and smaller planktivores. Importantly, the continued search to find new exploitable resources in our oceans may lead to increased pressure on non-traditional target species (e.g. mesopelagics, (Smith et al. 2011)), or an increase in effort in fisheries that are currently only lightly harvested (e.g. while krill is a focal species of Southern Ocean fisheries it is not yet intensively harvested through out its range). It is unclear, however, what impacts, both direct and indirect, can be expected if such increases in fishing pressure occurred. It is therefore important to look at the roles that the lower trophic groups play in fished ecosystems, and understand how increased fishing pressure on these groups will influence the systems of which they are part. In south-eastern Australian waters, and adjacent waters of the southern Pacific Ocean, two lower trophic groups of particular relevance, as they have high relative biomass and the potential for further exploitation, are squid and myctophid fish.

Globally, squid fisheries have increased substantially over the past 50 years (Caddy & Rodhouse 1998). This trend in squid fisheries is reflected in the Southern Squid Jig Fishery in Australia over the past 2 decades. The fishery began in 1986 with a single vessel, and has now increased to accommodate up to 43 fishing vessels in any one

season, with catches up to 435 tonnes a year (Lynch 2004). Such an increase in squid landings may be due in part to ecosystem impacts of fishing, where squid biomass increases due to a decrease in competition and predation from declining stocks of predatory finfish (Caddy & Rodhouse 1998, Myers & Worm 2003). It has been suggested that a consequence of an increase in squid stocks is that a further increase in landings may be both possible and sustainable (Caddy & Rodhouse 1998, Xavier et al. 2007). Squid, however, occupy an important role as both predator and prey in marine ecosystems (Smale 1996), thus it is important to understand the impacts of an increase in squid landings, both on the target species itself, and on predators, prey or competing species.

Another major potential resource are fish from the family Myctophidae. These fish are the dominant fish family, both in abundance and biomass, in the meso- and bathypelagic zones of the Southern Ocean (Pusch et al. 2004). It has been suggested that myctophids are a future target for fishmeal, fish oil and silage as traditional fish stocks continue to decline (Balu & Menon 2008). As a greater focus on aquaculture emerges in an effort to reduce pressure on traditional wild fish stocks (Verbeke et al. 2007), the high quality fish meal produced by myctophids could become a valuable resource for producing aquaculture stock feed. These mesopelagic fish play an important link in the pelagic food chain, being consumers of zooplankton, as well as a significant prey species for many marine predators (Uchikawa et al. 2002, Watanabe & Kawaguchi 2003, Pusch et al. 2004). Systems in which relatively few species form the link between the zooplankton and the higher level predators are referred to as ‘wasp-waisted’ (Cury et al. 2000). Myctophids may function as a key group in such a

system, similar to the role of planktivorous small pelagics – such as anchovies or sardines – in other systems (Cury et al. 2000, Shannon et al. 2000, Jordán et al. 2005).

Both squid and myctophid populations appear to have benefited from the reduction of predatory fin-fish species (Kitchell et al. 2002, Fulton et al. 2007), which suggests that they may become a potentially abundant oceanic resource. In this chapter, ecosystem impacts of increased fishing pressure on stocks of both pelagic squid and the myctophid fish located off south-eastern Tasmania are explored. The Atlantis ecosystem framework (Fulton et al. 2011) is employed to investigate the impact of different fishing scenarios, and to explore ecosystem impacts or changes in trophic structure resulting from increases in fishing pressure on myctophids and squid stocks. The aim of this study is to provide strategic insights into the consequences and potential ecological impacts that are associated with increased fishing pressure on these lower trophic groups. This chapter does not provide a strict assessment of the squid or myctophid stocks in south-eastern Tasmania, nor does it forecast the exact future of the relevant fisheries (if increased pressure was realised).

Methods

The Atlantis framework

Atlantis is a deterministic, biogeochemical ecosystem modelling framework (Fulton et al. 2004b). It tracks nutrient flows through the main biological and detritus groups within temperate marine ecosystems. The primary processes considered in Atlantis are consumption, production, migration, recruitment, waste production, habitat dependency, predation and (natural and fishing) mortality. The outputs of the model

consist of deterministic time series for each biological and spatial component in the modelled ecosystem.

This implementation of the framework will be referred to as the south-eastern Tasmanian Atlantis (SETas-Atlantis) model for the remainder of this thesis.

Biophysical realm

The domain of this Atlantis implementation covers approximately 265,000 km^2 of the waters off south-eastern Tasmania (Figure 2-1), and includes a diverse range of habitats. Soft sediment habitats, including sand, mud and seagrass form the dominant component of the area's inshore environment. Rocky reefs and kelp forests also play important roles in the ecology of the region. Offshore the model incorporates both shelf and open ocean environments. Ecologically, the area is highly diverse and contains a high proportion of endemic species. Pelagic primary productivity in the region is highly influenced by seasonal cycles (Harris et al. 1987).

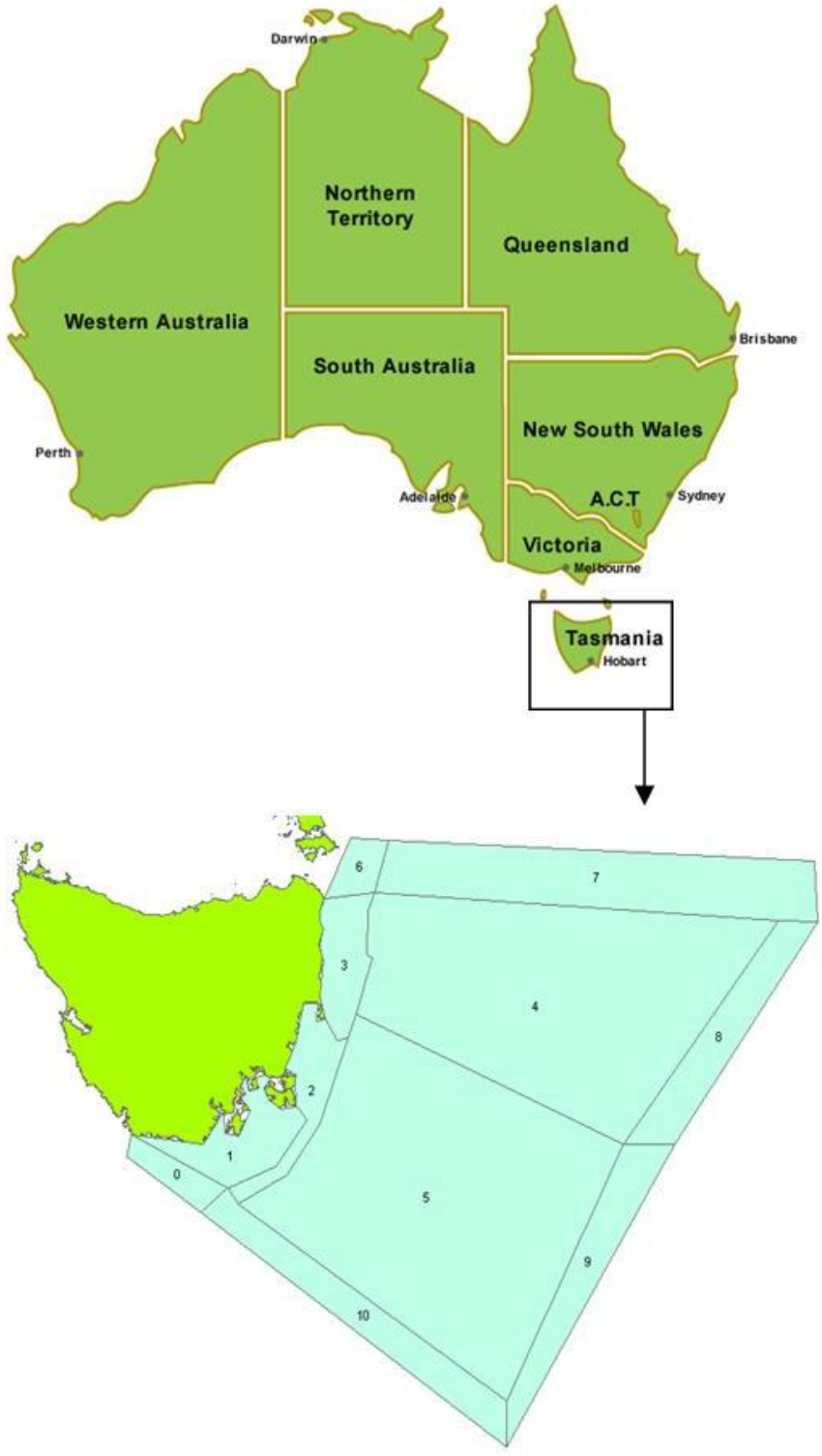

Figure 2-1. The spatial area of south-eastern Tasmania that is covered by the model domain.

The model is spatially defined both vertically and horizontally, using a 7 layer, 11 box geometry. A bioregion approach is used to resolve a spatial domain that is considered to be the minimum area necessary to represent the inshore/offshore regions inhabited by the groups of interest in this study (i.e. pelagic squid and myctophids). Within box spatial heterogeneity is also represented, with a fixed proportion of each habitat type (soft, reef, canyon and flat) allocated to each box. Any relevant habitat dependency is defined for each biological group, which acts to restrict the spatial domain of groups that are associated only with particular habitat types. By incorporating vertical stratification, we were able to incorporate the vertical migrations of biological components, and represent hydrodynamic and biological processes that vary with depth.

Biology

The biological groups included in SETas-Atlantis were made up of functional groups (aggregate groups of species with similar size, diet, predators, habitat preferences, migratory patterns and life history strategy) (Table 2.1). These biological components provide a representation of the entire foodweb; inshore and offshore, pelagic and demersal and from bacteria and phytoplankton up to top predators. The majority of the invertebrate and all the primary producer groups are represented using biomass pools, while the squid and vertebrates are represented as age structured stocks. In addition to these living biological groups, pools of ammonia, nitrate, silica, carrion, labile and refractory detritus are also represented dynamically.

Data for biological parameters such as initial abundance (Table 2-1), seasonal distribution, fecundity and timing of reproduction, growth and habitat preference, were obtained from a variety of sources including: the databases of the Central

Ageing Facility, Primary Industries Research Victoria (PIRVic); the Fishbase database (www.fishbase.org); re-parameterised from ecosystem models that encompassed the study domain (Fulton et al. 2007) and literature on the region (Kuiter 1993, Gomon et al. 1994, Edgar 1997, Taylor & Willis 1998, Edgar & Barrett 1999, Greely et al. 1999, Ewing et al. 2003, Edgar et al. 2004, Lyle et al. 2004, Barrett et al. 2007).

While all the fish groups in the model are represented as age-structured groups, squid are treated slightly differently. Because of the plasticity documented in arrow squid life history traits, especially individual growth rates, and age and weight at maturity (Jackson & Moltschaniwskyj 2001, Pecl 2001, Jackson & Moltschaniwskyj 2002, McGrath Steer & Jackson 2004), I have represented squid populations as two linked biomass pools (namely juveniles and adults), rather than using the more detailed age structured representation used for the vertebrate groups. This allowed the tracking of growth and reproduction at the population level (in terms of mg N m^{-3}), which is useful for stock management, without delving into the Pandora's box of individual variation in squid populations (Jackson & Moltschaniwskyj 2002). Therefore data for individual growth and reproduction rates was not required in this model. The percentage of nitrogen (N) per weight of squid was estimated at 10%, based on work by Villaneuva et al. (2004).

Table 2-1 Functional groups in SETas-Atlantis, their initial biomass values

Group name	Group composition	initial biomass (t)
Diatoms	Diatoms	3040732
Picophytoplankton	Picophytoplankton	16567450
Gelatinous zooplankton	Salps, coelentrates	3746517
Krill	Krill	904516
Copepods	Copepods	655168
Small zooplankton	Heterotrophic flagellates	3748595
Carvivorous infauna	Polychaetes mainly	1246740
Benthic deposit feeders	Polychaetes, some echinoderms (holothurians)	103895
Deep benthic filter feeders	Sponges, corals, crinoids, bivalves	183317
Shallow filter feeders	Oysters, other shallow filter feeders (e.g. corals and sponges)	12236
Urchins	Urchins	1224
Benthic grazers	Abalone and other grazers	2447
Macrozoobenthos	Crustacea (stompatopods, crabs), asteroids, molluscs, gastropods	329971
Commercial macrozoobenthos	Octopus, commerical crabs	19578
Meiobenthos	Meiobenthos	2077899
Macroalgae	Macroalgae	244724
Seagrass	Seagrass	2447
Squids	Squid	74930
Shallow demersal herbivores	Mullets, luderick, garfish, zebrafish, sea carp, dusky morwong, Rock blackfish	71102
Banded morwong	Banded morwong	283
Shallow territorial fish	Syngnathidae, Gobiidae (pipefish, seahorses, gobies etc)	2298
Shallow demersal fish	Flounder, gurnard, wrasse, snapper, whitings, latchet, flathead bream, morwong, trumpeter, toadfish, stargazers	48125
Other reef fish	Southern hula fish, leatherjacket, wrasses, mado, sea sweep, old wife, butterfly perch, bullseye	3237
Deep demersal fish	Deep demersal fish (dories, whiptails, hapuku, cardinalfish)	27506
Purple wrasse	Purple wrasse	949
Blue throat wrasse	Blue throat wrasse	557
Blue eye trevalla, warehou	Blue eye trevalla, warehou	601
Small pelagic fish	Anchovy, pilchard, sandy sprat, glassfish	2186
Mackerels	Mackerels	22098
Shallow piscivores	Bonito, yellowtail kingfish, teraglin, barracouta, mulloway	42573
Myctophids	Myctophidae	149047
Other mesopelagic fish	hatchet fish, lightfish	125328
Oceanic planktivores	Flying fish, sauries, redbait	80070
Oceanic piscivores	Tunas and billfish	5898
Dogfish	Dogfish	65313
Demersal sharks	Gummy shark, wobbygong, port jackso shark, sawshark	51756
Large pelagic sharks	bronze whaler, dusky whaler, blue shark, mako, white pointer, tiger shark	10264
Skates and rays	Skates and rays	1500
Baleen whales	Baleen whales	1366
Dolphins	Dolphins	497
Orcas	Orcas	756
Fur seals	Fur seals	536

Trophic Connections

The diet matrix used in Atlantis models defines the potential trophic connections between the different functional groups. It represents the potential accessibility of a prey item to a predator, rather than a definitive predation rate. Whether predation actually occurs depends on whether the predator and prey coincide both temporally and spatially (given mobility, habitat preferences and habitat state), the total amount of forage available (summing across prey groups) and whether the prey is of an appropriate size to be caught and consumed by the predator. Some predatory interactions are further divided by age class to represent the strength and rapidity of ontogenetic diet shifts that occur in some groups.

Data for the trophic connections are based on published information (O'Sullivan & Cullen 1983, Gales et al. 1993, Kuiter 1993, Gales & Pemberton 1994, Smale 1996, Edgar 1997, Bulman et al. 2001, Bulman et al. 2002, Uchikawa et al. 2002, Hume et al. 2004). The final values used were based on estimates from these sources, which were then modified through model calibration so that (i) the resultant realised diet composition matched the available data, and (ii) the time series trajectory generated by the model matched trajectories of available time series of observations.

Fishing model

While Atlantis has the capacity to incorporate dynamic fishing fleets, this study is a strategic investigation of simple increases in fishing pressure, therefore I simply enforced a constant fishing mortality rate on each fished group. This has the effect of increasing the proportion of the population that is landed, and removes some of the noise associated with variations in fishers' behaviour that a dynamic fishing model

can impose. A fishing mortality (F value) was estimated for each fished group by setting F to the proportion of the total population of each group that was taken as catch. Fishing pressure was imposed based on estimates of the annual rates of fishing by both federal and state fleets (Department of Primary Industries Water and Environment 2003, Fulton & Smith 2004). The final values used were modified from the reported catch values in the calibration process, in order to allow a stable biomass (i.e. no evidence of numerical instability) that simultaneously resembled biomass trajectories that were observed in the system over the past 10 years.

Model calibration

Time series trajectories of both biomass and abundance of many groups was constructed from data provided by the Tasmania Aquaculture and Fisheries Institute (Barrett et al. 2007). These time series showed biomass trajectories for reef species over 10 years, from 1992 – 2002. These time series were used to calibrate the trajectories of the reef groups in the model. For the groups where no time series data was available (e.g. the off-shore pelagic groups) the model was parameterised to obtain a stable system state with biological parameters that were within the values provided in the literature.

Scenarios

The major aims of this study were to investigate the impacts of two potential changes to the fisheries regime in the waters of south-eastern Tasmania. These were:

i. an increase in the fishing pressure on squid stocks
ii. the instigation of fishing pressure onto a currently unfished group, the myctophids

Table 2-2 outlines the specific fishing scenarios that were employed to investigate the above situations. The scenarios covered current fishing pressure and extreme fishing pressure that would cause a collapse of the squid or myctophid stocks, so that they were effectively removed from the system. This range of scenarios was designed to explore the impact on the surrounding ecosystem, rather than the impact on the fished stocks themselves. In each scenario all parameters were identical, other than the level of fishing pressure applied. All scenarios ran for the first 10 years without a change in fishing level to allow for model 'burn-in', then for a further 30 years with the perturbations imposed. Both adult and juvenile squid were fished, while myctophids were fished from age class 2 (i.e. from 2 years old).

Table 2-2 Scenarios examined in this study

No.	Scenario name	Specifications
1	Base fishing rate	Current fishing effort: - annual squid catch rate is 0.01 of total biomass - no fishing pressure applied to myctophids
2	High squid pressure	Annual squid catch rate is increased to 0.5 of total biomass
3	Squid stock collapse	Fishing pressure on squid increased to 0.9 of total biomass
4	High pressure on myctophids	Annual myctophid catch rate is 0.5 of total biomass
5	Myctophids stock collapse	Annual myctophid catch rate is 0.6 of total biomass

Results

The results of each scenario showed a proportional response in respect to the level of fishing pressure and the impact on other ecosystem components (i.e. any group that was heavily impacted from the collapse of squid or myctophids was also impacted by a lesser reduction in numbers of these groups, simply by a reduced degree). As such, only the results from the scenarios where the squid and myctophids stocks completely collapsed will be presented here.

The relative change in biomass of each group under both squid and myctophids collapse in comparison with the base fishing scenario is shown in Table 2-3. Note, as Atlantis is a deterministic model any changes seen in the scenarios where fishing regimes were altered are a direct result of this alteration, not a result of stochastic events.

Table 2-3 Ecosystem wide effects of the collapse of myctophids and of squid. Values represent the relative final biomass of each group in comparison with the final biomass of the base fishing scenario.

Group	relative change of final biomass with collapse of squid	relative change of final biomass with collapse of myctophids
Diatoms	1.00	1.00
Picophytoplankton	1.00	1.00
Gelatinous zooplankton	1.01	1.10
Krill	1.01	1.04
Copepods	1.00	0.94
Small zooplankton	1.00	1.01
Carvivorous infauna	1.00	1.00
Benthic deposit feeders	1.00	1.01
Deep benthic filter feeders	1.00	1.00
Shallow filter feeders	1.00	1.01
Urchins	1.00	1.00
Benthic grazers	1.00	1.00
Macrozoobenthos	1.00	1.00
Commercial macrozoobenthos	1.00	1.00
Meiobenthos	1.00	1.00
Macroalgae	1.00	1.00
Seagrass	1.00	1.00
Squids	0.00	1.01
Shallow demersal herbivores	0.99	1.00
Banded morwong	1.49	1.02
Shallow territorial fish	0.96	0.99
Shallow demersal fish	1.00	1.00
Other reef fish	1.00	1.00
Deep demersal fish	1.00	0.93
Purple wrasse	1.00	1.00
Blue throat wrasse	1.00	1.00
Blue eye trevalla, warehou	1.01	1.02
Small pelagic fish	1.04	0.74
Mackerels	1.00	1.05
Shallow piscivores	1.00	1.02
Myctophids	1.02	0.00
Other mesopelagic fish	1.07	1.02
Oceanic planktivores	1.01	1.01
Oceanic piscivores	1.00	0.87
Dogfish	1.00	1.00
Demersal sharks	0.96	0.98
Large pelagic sharks	0.98	0.89
Skates and rays	1.00	1.01
Baleen whales	1.00	1.00
Dolphins	1.00	0.99
Orcas	0.98	0.89
Fur seals	0.98	0.89

Impact on target groups

In regard to the impacts on the targeted groups, the squid population showed a considerable degree of density dependence, making them more robust to high levels of fishing pressure than were the myctophids. When fishing pressure on squid was increased to 50% of the biomass, the total biomass of squid (i.e. catch and unfished biomass combined) increased by approximately 30% from the base fishing rate scenario. Up to 85% of the squid biomass could be fished before the population became unviable. This pattern is likely to be due to high reproduction rates, short life spans and high levels of cannibalism found in the group. A limited increase in pressure on squid populations was beneficial to the stock, as cannibalism is reduced. This benefit, however, is not unlimited, and as fishing pressure is increased eventually the biomass drops as a result of the removal of spawning stock. Myctophids did not show this density dependence or degree of robustness, and collapsed under an annual fishing pressure of 0.6.

As expected, high levels of fishing pressure imposed on either the myctophids or the squid reduced the respective biomass of these groups.

Ecosystem impacts of squid stock collapse

The only groups that were impacted (by more than 2% of their biomass in the base fishing scenario) by the loss of squid from the ecosystem are: small pelagic fish, banded morwong, mesopelagic fish, shallow territorial fish, and demersal sharks (Figure 2-2). Small pelagic fish showed an increase in biomass of 4% as a result of the reduction in squid numbers. This increase was displayed as a higher abundance rather than any increase in size of individuals, and was caused by predation release from the

squid after their collapse. Banded morwong showed the greatest impact from the removal of squid stocks of 49%, despite being only a minor prey item. No change in the size or condition of banded morwong was seen, the increase was due to an increase in abundance, particularly of the juveniles as a result of predation release from the squid.

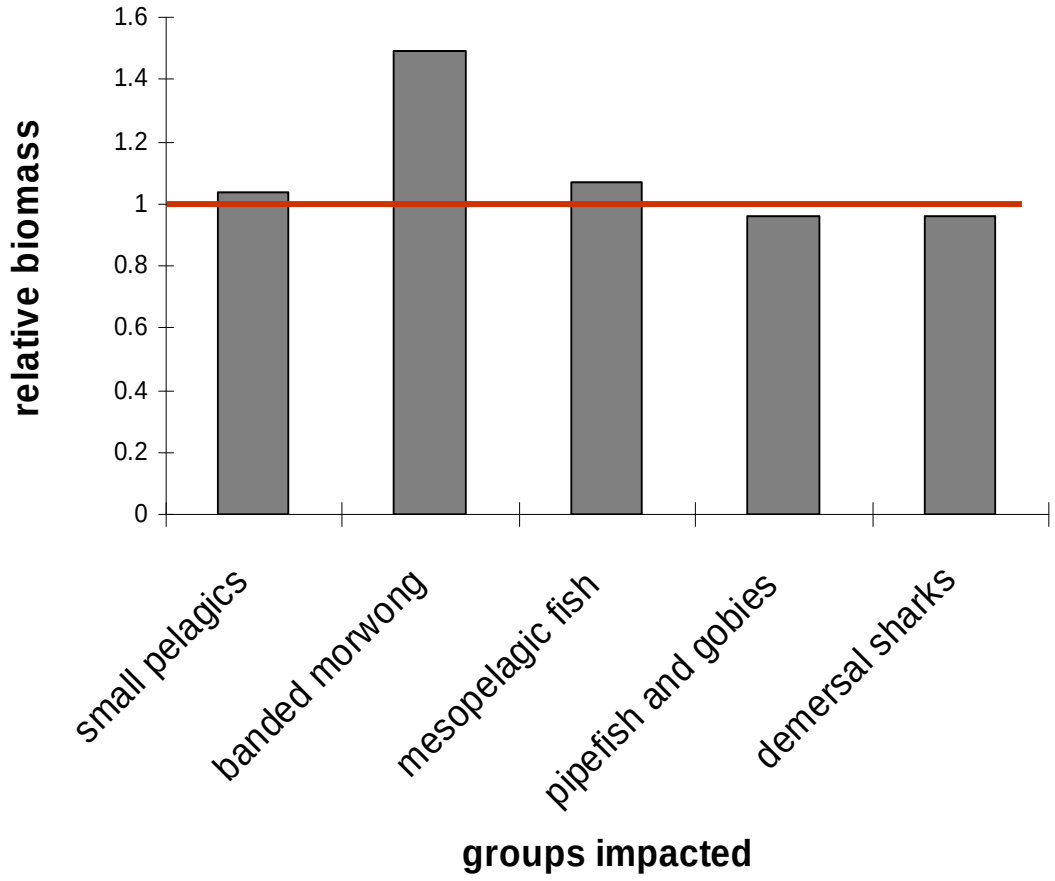

Figure 2-2 Proportion of initial biomass of impacted groups after 30 years in response to squid removal.

The mesopelagic fish also benefited from a reduction in squid numbers, increasing in abundance by 7% due to a release from predation. Groups that declined in biomass were the shallow territorial fish and the demersal sharks. Shallow territorial fish suffered an indirect reduction in abundance of 4% as a result of the collapse of the squid stocks. This occurred due to the switching behaviour of some of the piscivorous

fish; namely, shallow piscivores, shallow demersal fish, benthic sharks and pelagic sharks. The switch meant these predators consumed a larger proportion of these small fish due to the lack of available squid prey. Demersal sharks dropped in size by 4% in response to the reduction in squid as prey, but showed no change in abundance. This reduction in size is more pronounced in the juveniles than the adults (the weight of the juveniles drops by 6%, whereas the adult weight drops by only 2%), indicating that squid is a more important prey item for the juveniles of this group.

Ecosystem impacts of myctophid stock collapse

The groups that were impacted by the loss of myctophids from the ecosystem were: mackerel, small pelagic fish, large piscivores, deep demersal fish, pelagic sharks, seals, orcas, krill, gelatinous zooplankton and copepods (Figure 2-3). The mackerel showed an overall biomass increase of 5% with the collapse of myctophids, increasing in both abundance and size. Juvenile mackerel showed the largest change in size (an increase of 4%), which was caused by the release from competition from myctophids. The anchovies and whitebait suffered a 25% reduction in biomass after the collapse of the myctophid stocks. The adults of this group were the most heavily impacted, with their population abundance reduced to 40% of the population in the control scenario. This was due to the more severe predation pressure once their predators' alternate prey of myctophids was removed. The large piscivorous pelagic fin-fish group stabilised at an 8% lower biomass with the higher pressure on the myctophids, which was caused by a reduction in size as a major prey source was lost, however there was no drop in abundance of this group.

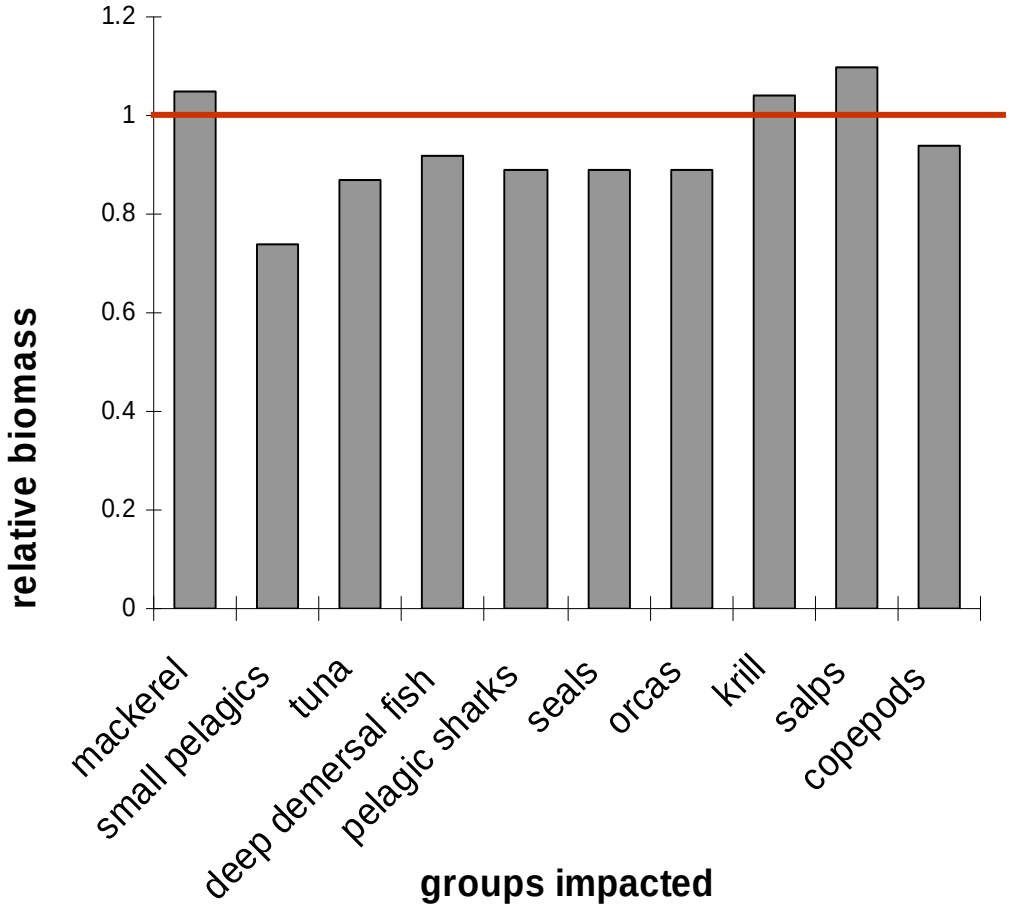

Figure 2-3. Proportion of initial biomass of impacted groups after 30 years in response to myctophid removal.

The juveniles of the deep demersal fish reduce in abundance by 7% without the myctophids, due to the higher predatory pressure from piscivorous fish. This increase in pressure only occurs in the final ten years of the run, which coincides with a steeper decline in the small pelagic group. At this point the juveniles from the deep demersal group replace (to some degree) the diminishing population of small pelagic fish as a prey source for the large piscivores. Pelagic sharks also show a substantial drop in biomass of 11%, which is caused by a reduction in size, rather than a decline in abundance. Juveniles of this group are especially impacted, dropping to 73% of their weight in the control scenario (with status quo fishing pressure), which is putting them close to the kind of body condition where starvation mortality will start to take a

toll. Both the seals and orcas show a similar pattern, dropping in weight by 10% and 11% respectively across all age classes, but showing no reduction in abundance.

As expected, both krill and gelatinous zooplankton biomass increase due to the predation release that accompanies the removal of the myctophids, krill by 4% and gelatinous zooplankton by 10%. The mesozooplankton biomass, however, drops by 6% in response to the increased predation pressure from the higher volumes of gelatinous zooplankton and krill.

Discussion

Ecological Implications

In SETas-Atlantis the removal of myctophid fish causes a greater impact on more of the functional groups than does the removal of squid. Although there is a slight change in biomass of some groups under the high squid pressure scenarios, it is minimal in comparison to the scenarios where myctophids are significantly reduced. Some restructuring of trophic linkages is associated with the removal of squid from the system. The most obvious is an increase in predation on the territorial reef fish, which occurs when squid are removed and carnivorous fish focus on alternative prey sources. In general however, the ecosystem appears to be robust to increased pressure on squid. Although squid have a high biomass and play a substantial role as both predator and prey in this marine ecosystem, their generalist nature in both of these roles means their removal does not cause a significant change to the ecosystem. No known predators consume squid to the exclusion of other prey items (Smale 1996). Thus, a reduction in squid numbers simply leads to an alteration in proportion of prey

items for any one predator, as other groups move in to fill the niche left by the squid. Similarly, as squid are themselves predators of many fish species, the reduction in their numbers actually benefits many fish; both directly from a release from predation, and indirectly, by increasing the prey available (i.e. by a reduction in competition).

With the removal of myctophids however, comes a more substantial alteration to trophic linkages within this ecosystem model. The removal of myctophids reduces predation on krill and gelatinous zooplankton, which has cascading effects throughout the trophic web. Larger planktivorous competitors such as mackerel benefit from the increased food supply. Smaller planktivores however, suffer a much stronger pressure from predators such as seals, small chondrichthyans and large piscivorous fish. This reduction in small pelagic fish abundance further reduces pressure on zooplankton, creating a positive feedback loop, where less and less of the system's productivity is being passed to the higher trophic levels. The seals and large piscivorous fish in turn suffer from the vastly reduced prey source with the removal of the myctophids, and reduction of other small planktivores. The impact of the reduction in biomass of the piscivorous fish and pinnipeds then extends through the foodweb to the highest trophic groups in the system. The reduction in orca and pelagic shark biomass is the result of a reduction in these prey groups. So, from zooplankton up to orcas, a clear reduction in the trophic flow in this system can be seen in these simulations.

The results presented here support the view that the ecosystem as parameterised here fits under the wasp-waisted system structure, that is myctophids are one of the few links between plankton and higher trophic groups (Cury et al. 2000, Shannon et al. 2000). Shannon et al (2000), found that the ecosystem impacts of high fishing

pressure on small planktivorous fish in such systems depend on whether the system is bottom-up controlled (i.e food resources limit population numbers) or top-down controlled (i.e. predation limits population numbers). This duality is seen because in bottom-up controlled systems small pelagic planktivores are limited by their food source making their populations density dependant. Increasing the mortality of these fish has the dual effects of reducing density dependence, whilst also allowing competing (similarly food limited) planktivorous species to increase at a more rapid rate and fill the newly available niche. It therefore does not lead to the loss of the important link between plankton and higher trophic groups seen in a top-down controlled system.

The levels of primary production from phytoplankton in this region suggest that the ecosystem may be top-down controlled at times. However, the high fluctuation of productivity on a seasonal basis (Harris et al. 1987) may lead to seasonally-driven bottom-up control of the system. In this model phytoplankton was parameterised so that it did not become limiting. However, other parameterisations of the model where phytoplankton biomass was significantly reduced (thereby creating a bottom-up controlled system) produced different results, specifically a reduction in impact from the removal of myctophids. Future work could address the impacts of fishing in a system where phytoplankton biomass fluctuated, causing the system to switch seasonally between top-down and bottom-up control.

The results presented here are similar to those obtained by Cury et al.(2000) Shannon et al (2000) and Smith et al.(2011), who showed that heavy exploitation of small pelagic fish in a highly productive system can lead to an increase in their prey and a decrease in their predators, causing a disruption in the trophic flow in the system.

There is a danger in targeting the critical link between higher and lower trophic groups in any ecosystem. This link however can differ from system to system. While anchovies, sardines and herrings perform this role in system such as southern Benguela, it appears that southern Australia is particularly dependant on myctophid fish, as the relative magnitude of abundance of small pelagics is much smaller in this system than in other (e.g. upwelling) systems.

Caveats

The SETas-Atlantis is a simplified representation of the south-eastern Tasmanian ecosystem and the fisheries that occur there. Fishing pressure in this model study is uniform, both spatially and temporally, and doesn't take into account switching behaviour of fishers, or reduced fishing pressure when stocks become limited. Similarly, the ecosystem is assumed to be in a relatively stable state in the control run (i.e. no groups are in a state of serious decline or uncontrolled growth). Having a stable control state allows a clearer examination of the impacts to the system under the treatment scenarios, than would a system that is already seeing the collapse of some of the fisheries. It is assumed that, although this may not be an exact representation of the current state in south-eastern Tasmania, the stability would have been a feature of the system prior to heavy fishing. Therefore the results are representative of a state that has been perturbed by fishing and provide a strategic insight into the kinds of impacts that would be expected from a reduction in biomass of the key groups examined. Further work could incorporate a more realistic fishing effort in the model and a more refined treatment of some of the groups. For instance there is evidence that tuna stocks are rapidly diminishing from this area, potentially as

a result of fishing and environmental pressures (Galeano et al. 2005). A more detailed representation of the relevant fisheries and groups could clarify whether the results presented here are maintained when large piscivores such as tuna are heavily fished (or declining for other reasons). Nevertheless, although the quantity of impact may be uncertain, the direction of the changes is realistic and informative.

Conclusion

The introduction of a myctophid fishery may have serious consequences for this ecosystem, removing a vital link between lower and higher trophic groups. Although this fish could potentially provide a cheap, abundant and high quality stock feed for aquaculture, the risks to the ecosystem suggest that there would be a high ecological price to pay for this economic gain. An increase in landings of squid stock on the other hand may have much less of an impact on the ecosystem as a whole, although the alternative parameterisations of the model would need to be explored to be certain of this result. While it is beyond the scope of this study to consider what a sustainable level of fishing on squid would be, a high level of pressure does not appear to cause a large shift in the trophic structure or ecosystem dynamics of this system.

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Chapter 3. The use of telescoping spatial scales to capture inshore to slope dynamics in marine ecosystem modelling

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Natural Resource Modeling 24:335–364

Chapter 4. Implications of model parameterisation and spatial structure when assessing the ecosystem impacts of a reduction in pelagic forage species

Introduction

The global trend in world fisheries is that we are fishing both down (Pauly et al. 1998) and through (Essington et al. 2006) the marine food web. The continued search to find new exploitable resources in our oceans is leading to increased pressure on non-traditional target species, or to an increase in effort in fisheries that are currently only lightly harvested, such as smaller planktivores, mesopelagics or lower trophic level invertebrates like krill.

Forage species (also referred to as low trophic level species) have been shown to exert a substantial influence in many ecosystems, forming an important link between higher and lower trophic levels in marine food chains. Systems in which relatively few species form the link between the zooplankton and the higher level predators are referred to as 'wasp-waisted' (Cury et al. 2000). Previous studies have shown that depletion or loss of these key species has the potential to disrupt the ecosystem, with impacts cascading from the top of the food chain down to the primary producers (Shannon et al. 2000, Estes et al. 2011).

The impact of a reduction of these key species is becoming more relevant, as fisheries increasingly target small, often previously unharvested species to provide fodder for aquaculture (Merino et al. 2008). At first consideration, small pelagic planktivorous

fish are prime candidates for higher catches, given their high inherent productivity coupled with relatively high biomass in many ecosystems. However despite these promising attributes, it is unclear what the broader ecosystem impacts of an increase in fishing pressure on these species will be. Given their crucial roles in ecosystem function (Cury et al. 2000, Shannon et al. 2000), it is important to investigate how fishing on these groups will impact species at both higher and lower trophic levels, including other economically important species as well as protected and iconic species.

Ecosystem models are becoming a more widespread tool that can be used to help address questions concerning ecosystem impacts of fisheries management decisions. However, the structure (both in terms of model size and trophic structure) of any chosen ecosystem model may have impacts on the results provided by the model. Spatial structure is of particular importance when examining fishing scenarios and management of stocks, because habitat refuges and spatial distribution of predators and prey species may have an impact on trophic interactions and therefore on ecosystem structure. So, the examination of the role of forage species in marine systems may be impacted by how a model is spatially constructed. In order to address this concern, this chapter uses 3 different spatially structured Atlantis ecosystem models to examine the impact of high levels of fishing pressure on forage species, and how this depletion affects the surrounding ecosystem. The results are compared to explore both the similarities and differences found between the models. This is then put into context with regard to fisheries management strategies and what guidance these model simulations can provide in terms of potential system impacts of fishing lower trophic level species.

In part, this chapter will replicate the work from chapter 2, but using alternative model structures (and incorporating further lower trophic level groups in the depletion experiments). This work aims to explore whether the results obtained from a spatially simple model (SETas-Atlantis) can be replicated using models with a more complex spatial domain. Is a larger area required to investigate impacts in a relatively small area, or does this extra model domain simply add further complexity and noise?

Methods

In order to gain a more comprehensive understanding of the impact of reducing the abundance of forage species in marine ecosystems four different Atlantis models were employed. These differences consisted of 3 different model spatial structures with one spatial structure parameterised using two different sets of biological data. The spatial domain of each model is shown in Figure 4-1. The Atlantis-SM (ASM) model sat wholly within the domain of Atlantis-SE (ASE), and the Atlantis-SETas (SETas) model was nested within the domain of ASM. In some cases the different models used identical box structure and thus only the red outlines can be seen for these boxes in Figure 4-1.

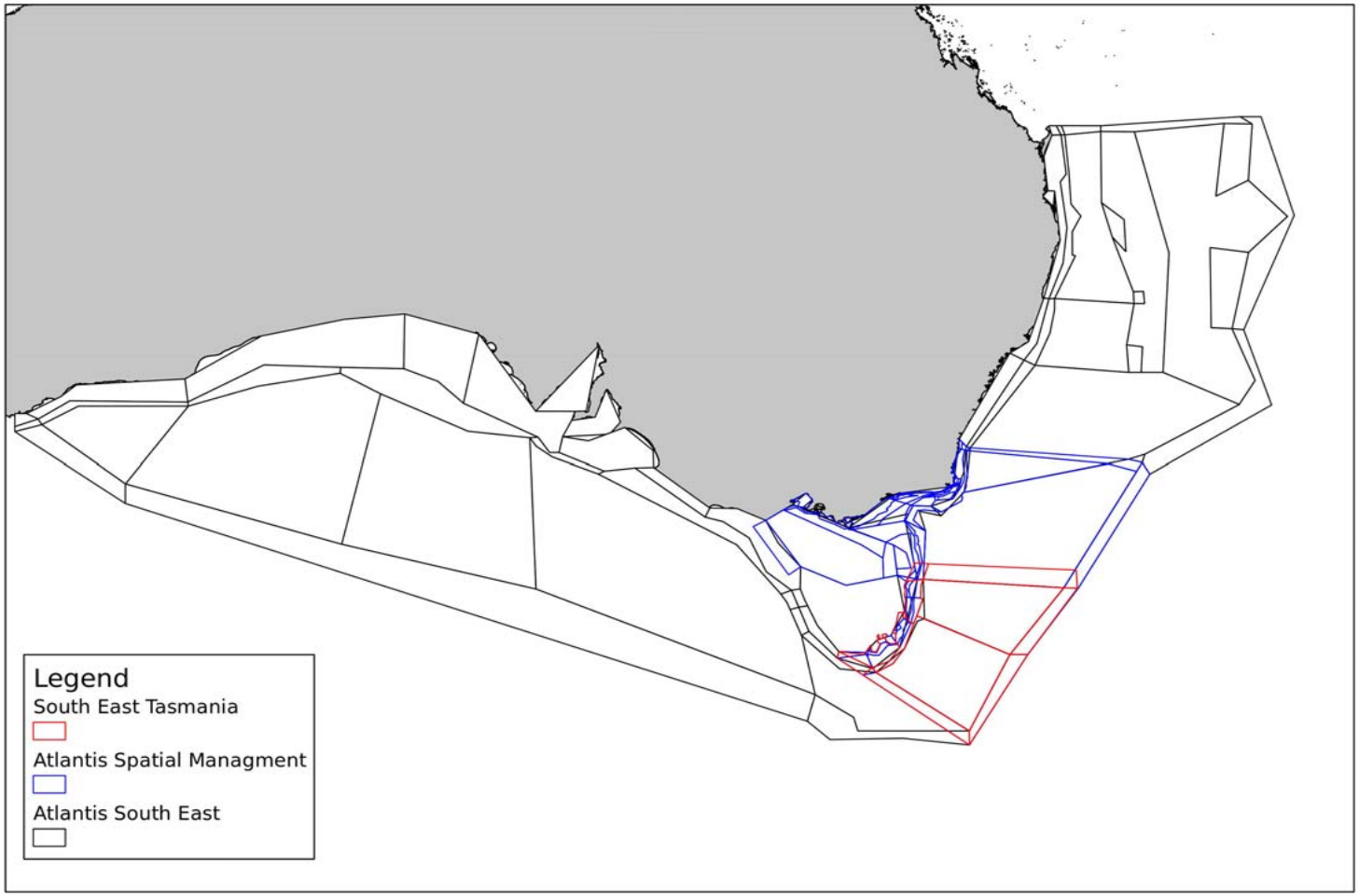

Figure 4-1. The spatial domain and structure of each of the three models: South East Tasmania (SETas), Atlantis Spatial Management (ASM) and Atlantis South East (ASE)

Models

The models were based on the Atlantis framework (Fulton et al. 2004b, Fulton et al. 2011). Processes such as production, consumption and growth, habitat dependency, reproduction, movement and large-scale migration, predation and other forms of mortality and waste production are all handled explicitly. The trophic resolution is either at the functional group level or at the species level. The outputs of the model consist of deterministic time series for each biological component in the modelled ecosystem, driven by fishing pressure on various species and functional groups.

Two of the models used covered the same spatial domain. These models are two versions of the Atlantis South East model (ASE), which was previously developed to explore alternative strategies for management of south-eastern Australian fisheries (Fulton et al. 2007). The model domain is the southeast regional ecosystem, which covers 3.7 million km^2 of the waters within Australia's south eastern EEZ. In this study the original model is referred to as version 1 (ASE v1). The second version of the model (ASE v2) varied in the parameterisation of the dietary connections between groups so that there was an increased dependence on the lower trophic fish groups as a food source for most of the piscivorous groups, as well as a higher biomass of myctophids (by approximately an order of magnitude). ASE v2 was created so that alternative, realistic empirical data could be used in the parameterisation, which emphasises the importance of myctophids within the system. Although both versions of ASE were parameterised using realistic data from the literature, because there is often a great range of data that must be condensed to a single value during the

parameterisation (especially in regard to dietary connections and absolute biomass), it was interesting to see how different versions of the same model would behave.

The third model used for these evaluations was the Atlantis Spatial Management model (ASM). This model was previously developed as a means of modelling a large spatial domain without excessive spatial complexity (see chapter 3 for full details). The model domain covers approximately 640,035km^2 off the south-east coast of Australia. The domain extends from north of the New South Wales-Victorian border to just west of Port Phillip Bay, and around the Eastern side of Tasmania, including all of Bass Strait. This model was parameterised very similarly to version one of the Atlantis SE model, with the main difference being the size of the model domain.

The fourth model, Atlantis SE Tasmania (SETas), covered a smaller spatial domain still, and covered only 265,000 km^2 the waters off south eastern Tasmania. Again, this model was parameterised very similarly to both the ASM and ASE v1.

Scenarios

Scenarios were examined where a large increase in fishing pressure was imposed on 3 lower trophic groups. In each scenario, one of these species or groups was subjected to very high fishing pressure, to the point where that group became effectively extinct. These scenarios were run with increased fishing on; a) small planktivores (anchovies, sardines), b) large planktivores (mackerel) and c) migratory mesopelagics (myctophids).

Although the parameterisation was kept as consistent as possible in all models (except the diet parameterisation in ASE v2), some differences in relative initial biomass, as well as the biomass trajectories, were inevitable due to the spatial domain that each model covers. Table 1 shows the biomass of the above groups at year 10 as a proportion of total ecosystem biomass in each model.

Table 4-1 Relative overall biomass contribution for the group at year 10 in each model

	ASEv1	ASEv2	ASM	SETas
small pelagics	7.17E-06	7.17E-06	5.54E-04	1.15E-05
myctophids	5.78E-06	4.35E-05	1.48E-04	1.42E-03
mackerel	4.69E-06	4.71E-06	4.63E-05	1.79E-04

Model simulations were initiated at 2005 biomass estimates and fishing levels and projected the model forward for 20 years. As the dynamics of the lower trophic levels can still show significant transient dynamics on start-up, a 'burn-in' period of 10 years was run with a constant fishing mortality on all groups, which was close to current status-quo fishing pressure for each groups, followed by a projection period of a further 10 years, during which altered fishing mortality were applied to the group of interest (with the level dependant on the scenario being explored).

Results are presented against a 'control scenario', where no group suffers a collapse and all groups are fished at 'status-quo' levels. The final biomass was taken as the average biomass over the final 5 years of the run to account for inter-annual variation within each group. The results are presented for each of the scenarios and each of the models as the biomass of impacted groups relative to their biomass in the base case.

Thus, any value over one is a relative increase in biomass, and any value less than one is a relative decrease.

Results

The results from each of the models differed to some degree, depending on the spatial structure and the parameterisation. Table 4-2 shows the impacts of each scenario in each of the models, showing which groups were impacted and the change in their final biomass relative to their final biomass in the control scenario.

Table 4-2 Summary table showing the impacted groups and relative change in biomass of these groups in each model and each scenario.

Model	Scenario	Groups impacted	Final biomass of group relative to control scenario
ASE - v1	Small pelagic collapse	orcas	0.98
		dolphins	1.05
		seals	0.95
		school shark	1.13
	Mackerel	orcas	0.98
		skates and rays	1.11
		small piscivores	1.07
	Myctophids	none	
ASE - v2	Small pelagics	shallow piscivores	0.89
		redbait	0.83
		seals	0.97
		orcas	0.96
		pelagic sharks	0.98
	Mackerel	small pelagics	1.08
		shallow piscivores	1.12
		lightfish	0.95
	Myctophids	mackerel	1.09
		small pelagics	1.78
		gemfish	0.79
		shallow piscivores	1.63
		lightfish	0.69
		redbait	1.36
		shallow demersal fish	1.10
		skates and rays	1.32
		gulper sharks	0.97
		dolphins	0.70
		orcas	0.84
		pelagic sharks	0.57
ASM	Small pelagics	mackerel	1.09
		lightfish	1.06
		skates and rays	1.03
		seals	0.94
		dolphins	0.92
		orcas	0.94
		shallow piscivores	1.04
		skates and rays	1.03
	Mackerel	none	
	Myctophids	light fish	0.98
		deep demersal fish	0.92
		demersal sharks	0.99
		seals	0.98
SETas	Small pelagics	none	
	Mackerel	none	
	Myctophids	mackerel	1.05
		small pelagics	0.74
		tuna	0.87
		deep demersal fish	0.92
		pelagic sharks	0.89
		seals	0.89
		orcas	0.89
		krill	1.04
		salps	1.10
		copepods	0.94

ASE - v1

Small pelagics

A collapse of small pelagics has impacts only on the higher trophic groups, in particular the seals, dolphins, orcas and some sharks (Figure 4-2). In all cases the impact was very small, and therefore there was no corresponding cascade throughout the food web when small pelagics were depleted. This response was because small pelagics only constituted a small part of the diet of each of these predators, and the loss of this prey was taken up by an increase proportion of other prey. Figure 4-3 shows the diet composition of orcas as an example, where shallow demersal fish expand to fill the gap left by the small pelagic fish.

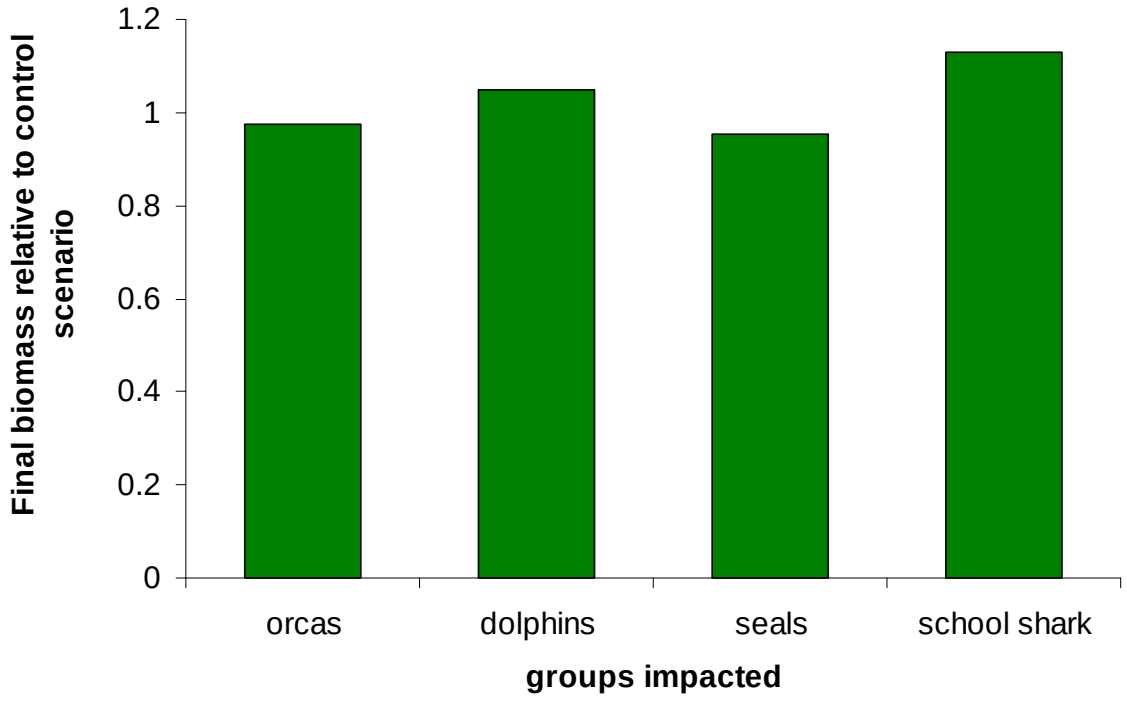

Figure 4-2 Biomass changes resulting from the collapse of small pelagics in ASE v1

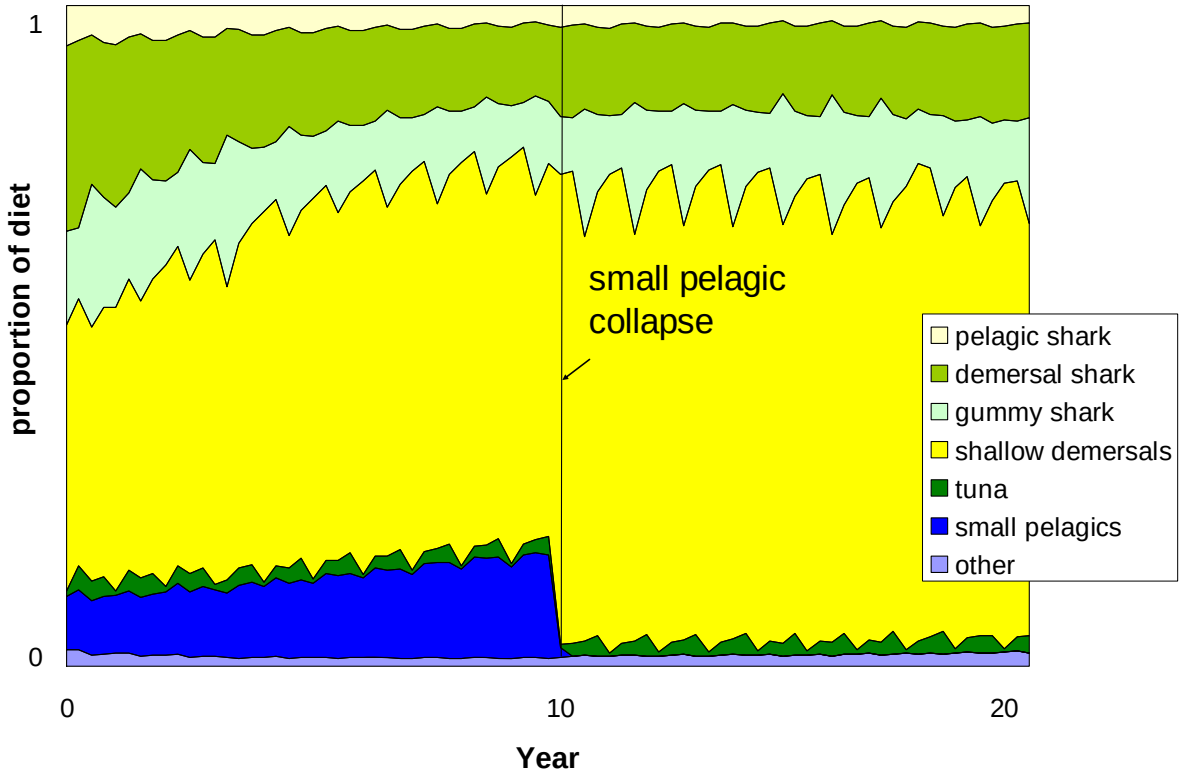

Figure 4-3 Aggregate diet composition (across all age groups and across the entire model domain) of orcas with the collapse of small pelagic fish.

Mackerels

The collapse of the mackerel had very little impact, other than slight impacts on the predatory groups small piscivores, skates and rays and dolphins (Figure 4-4). As with the collapse of the small pelagics, there were no changes in the trophic linkages with the collapse of the mackerel.

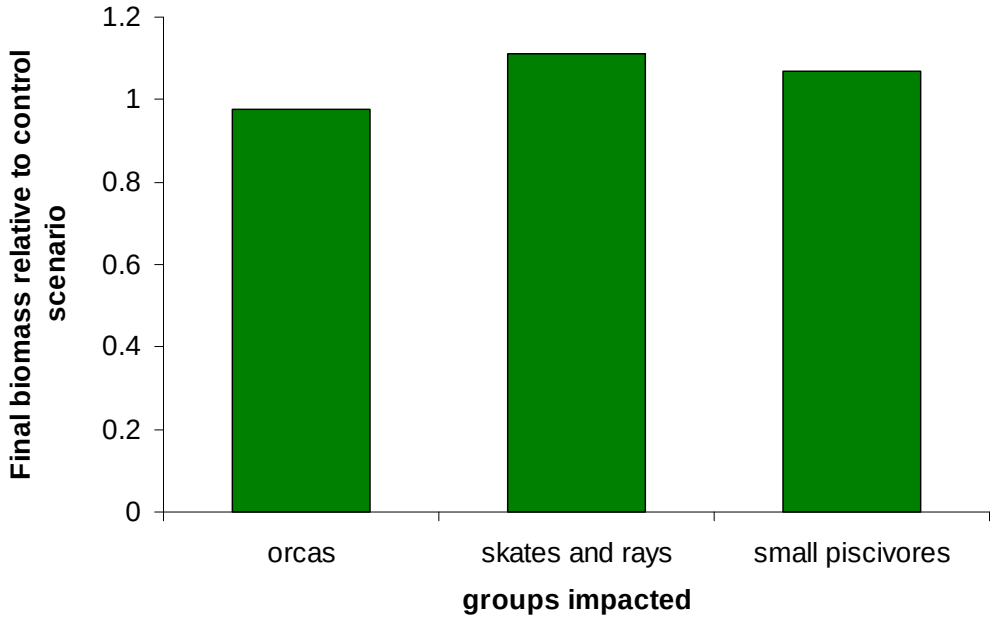

Figure 4-4 Biomass changes resulting from the collapse of mackerel in ASE v1

Myctophids

The collapse of myctophids had no noticeable impact on the ecosystem in this model. No groups or species varied in biomass from the base case scenario.

ASE - v2

Small pelagics

As with ASE-v1 the impacts due to the loss of small pelagics were relatively small at a system level. All the groups that are impacted by the loss of small pelagics show a reduction in overall biomass. The groups impacted were the small piscivores, red bait, seals, orcas and pelagic sharks (Figure 4-5). Nearly all of the groups impacted were predators of small pelagics; shallow piscivores, seals, toothed whales and pelagic sharks. The exception to this is the reduction in redbait, which is a prey item of all the other impacted groups. Interestingly, mackerel and shallow demersal fish also increase predation slightly on this group (Figure 4-6).

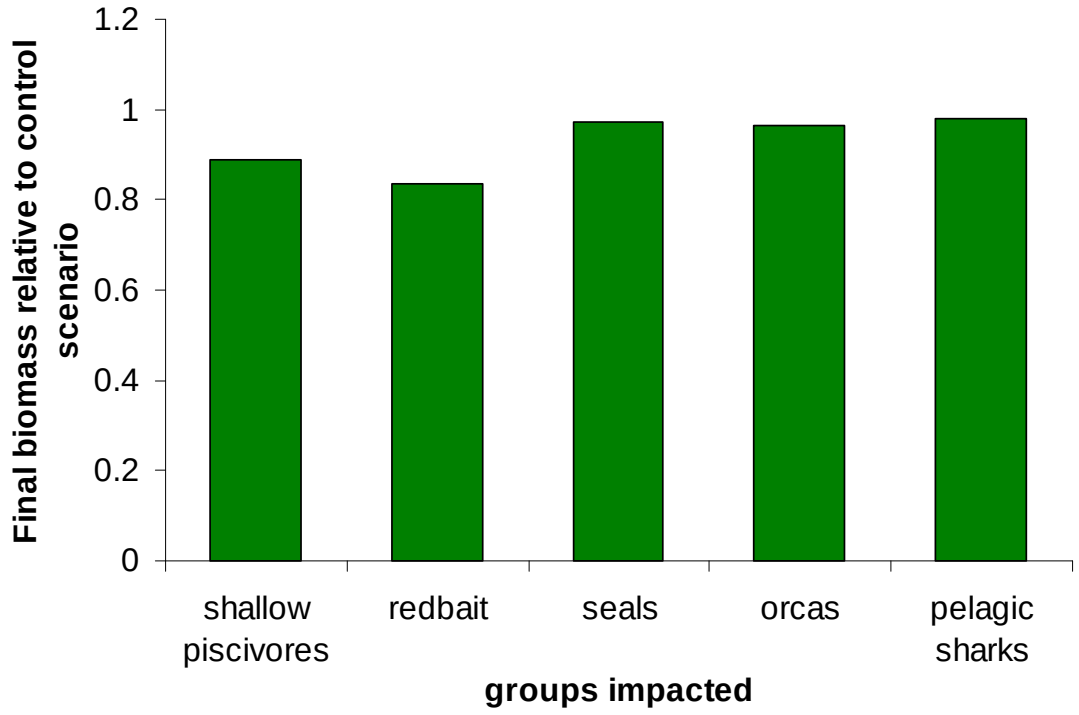

Figure 4-5 Biomass changes resulting from the collapse of small pelagics in ASE v2

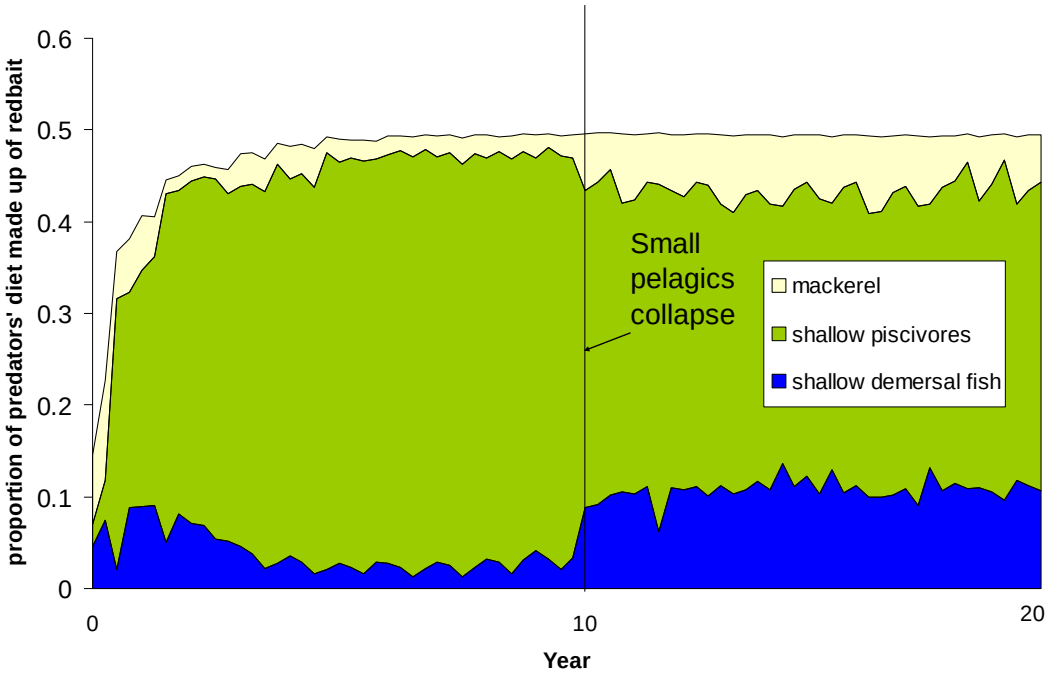

Figure 4-6 Proportion of mackerel, small piscivores and shallow demersal fish diets made up of redbait with the collapse of small pelagics

Mackerel

Figure 4-7 shows the changes in biomass that accompany the collapse of the mackerel group in ASE v2. The only groups that were impacted were the small pelagics, the small piscivores and the lightfish. The changes in biomass were small, with no group impacted by more than 10%. Because of this there was very little discernable change to the trophic connections as a result of the mackerel collapse.

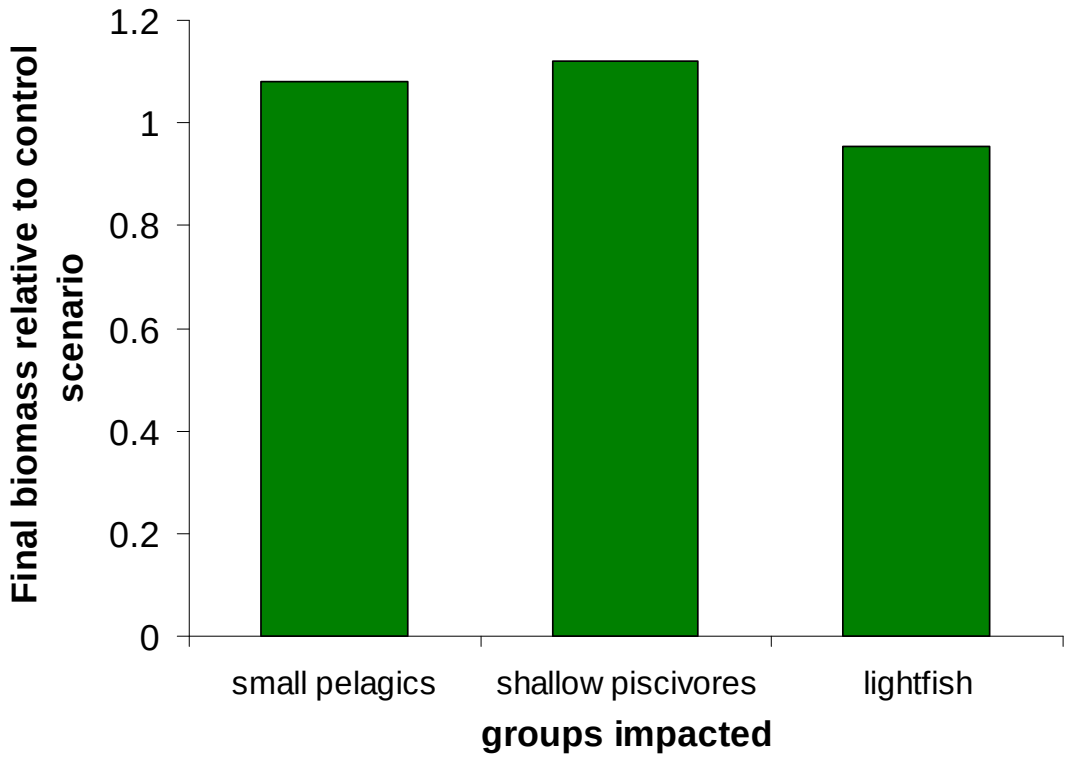

Figure 4-7 Biomass changes resulting from the collapse of blue mackerel in ASE v2

Myctophids

In this version of the ASE model there is a larger impact from the removal of some of the mid-trophic groups. The removal of the myctophids leads to a substantial change in the biomass of some of the higher trophic groups (Figure 4-8). Both pelagic sharks (Figure 4-9) and dolphins (Figure 4-10) had a high proportion of myctophids in their diet and consequently saw a large reduction in biomass when this prey source was removed. This led to an increase in predation on both gemfish and lightfish, which caused a reduction in these species' biomass. However, the reduction in predator biomass lead to an increase in some prey groups. Small pelagics (Figure 4-11) and shallow piscivores (Figure 4-12) benefit from the reduced predation pressure from the pelagic sharks. Interestingly, both pelagic sharks and orcas switch to feeding more heavily on lightfish once the myctophids populations collapse (Figure 4-13). Lightfish also suffer from the removal of a prey source in the juvenile myctophids, so this species is impacted from the loss of prey, in conjunction with increased predation pressure. Shallow piscivores switch predation from redbait to lighfish, which has a higher biomass than the redbait (Figure 4-14). In turn this results in an increase in redbait biomass, as shallow piscivores were their major predator.

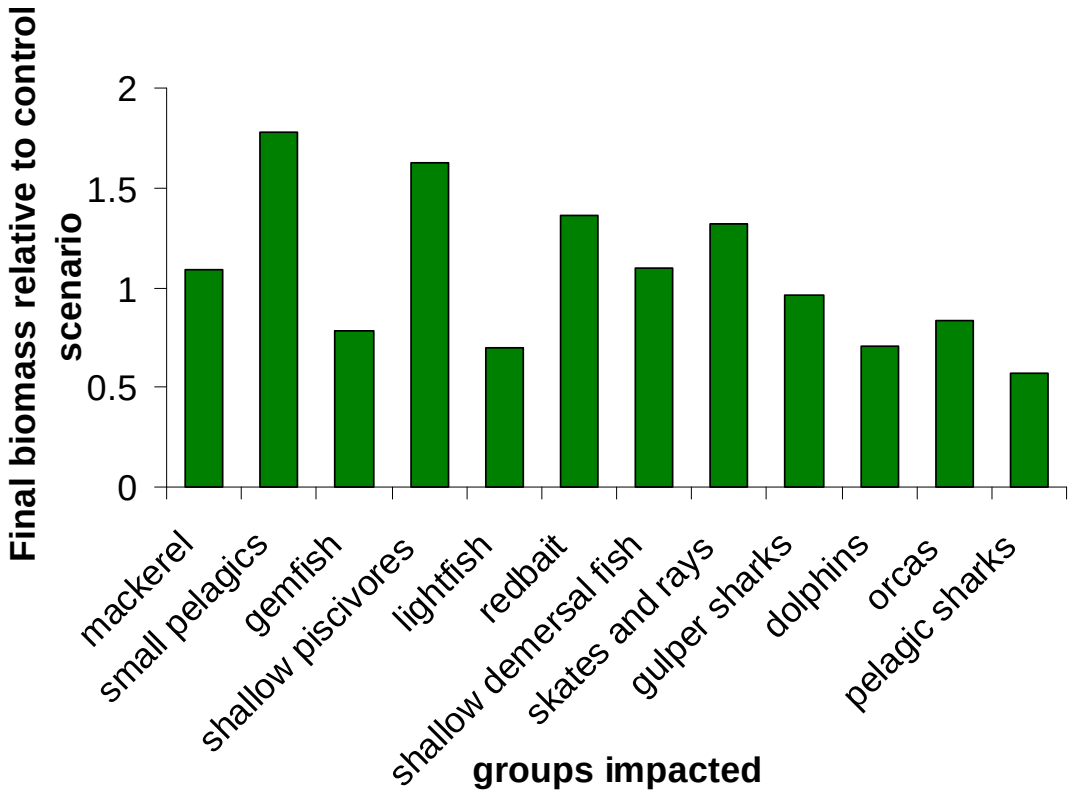

Figure 4-8 Biomass changes resulting from the collapse of myctophids in ASE v2

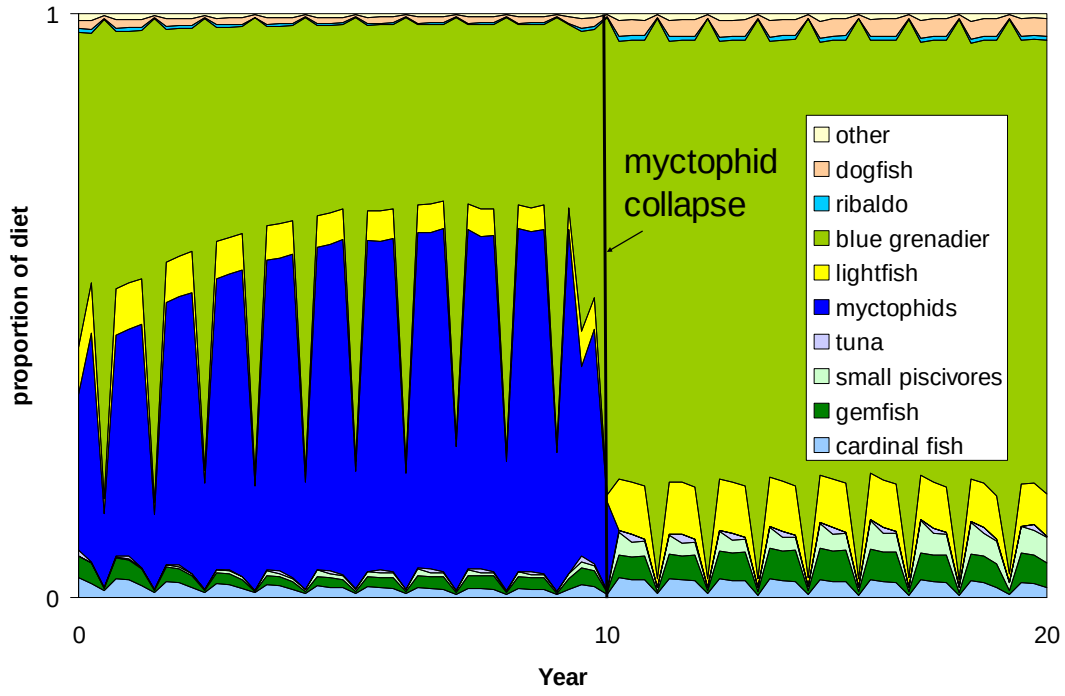

Figure 4-9 Aggregate diet composition of pelagic sharks with the collapse of myctophids.

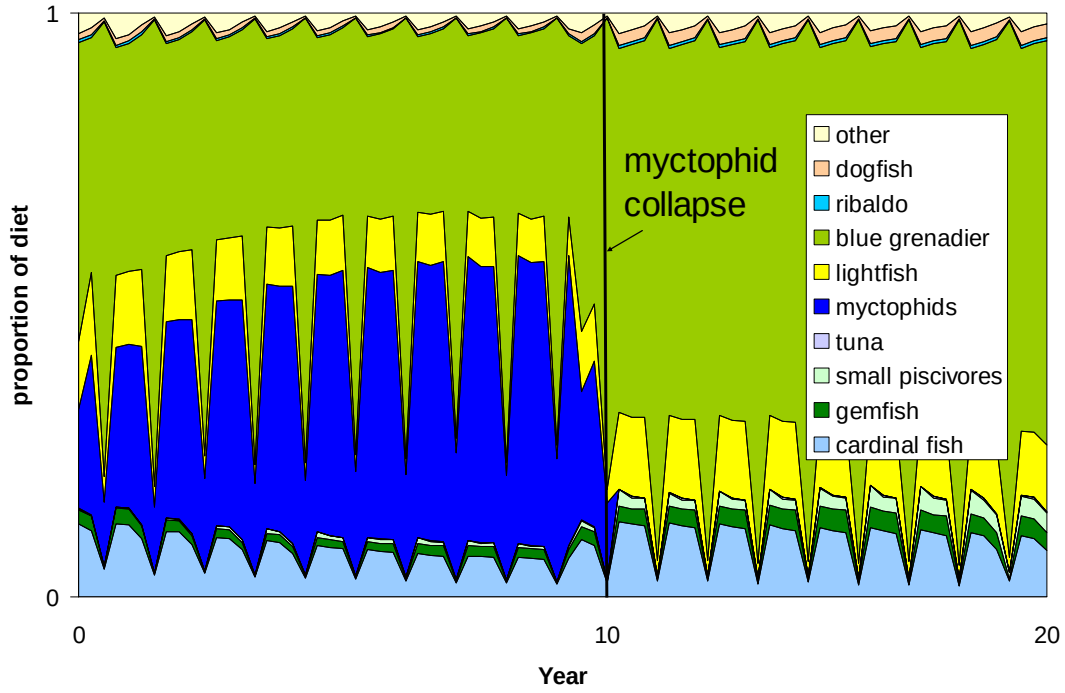

Figure 4-10 Aggregate diet composition of dolphins with the collapse of myctophids

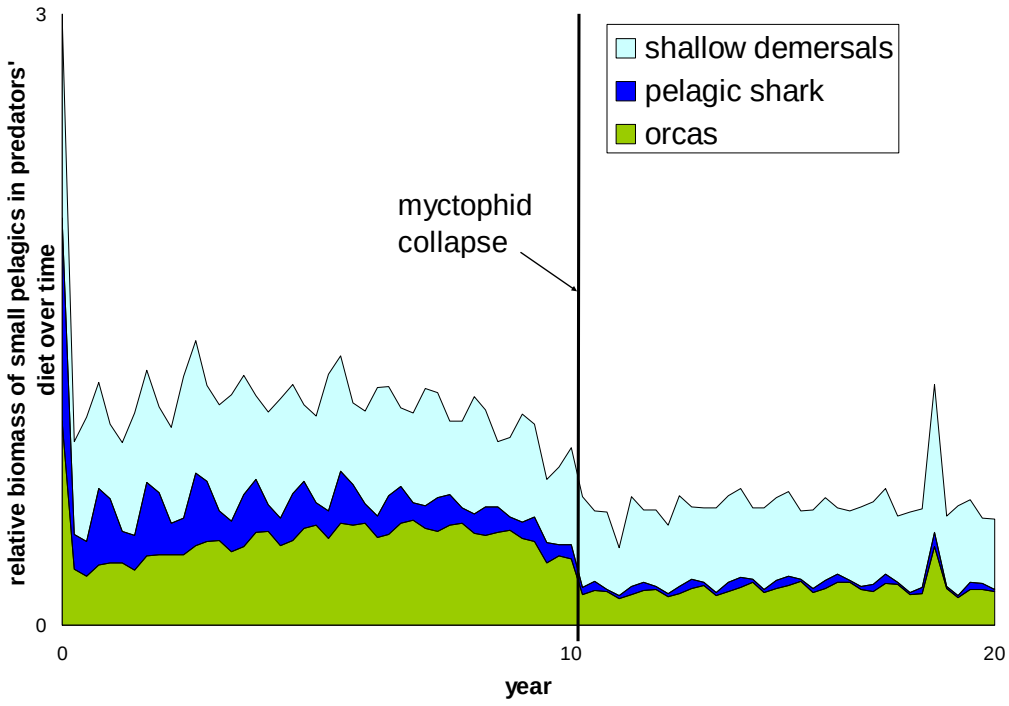

Figure 4-11 Changes in the predation pressure on small pelagic fish with the collapse of myctophids

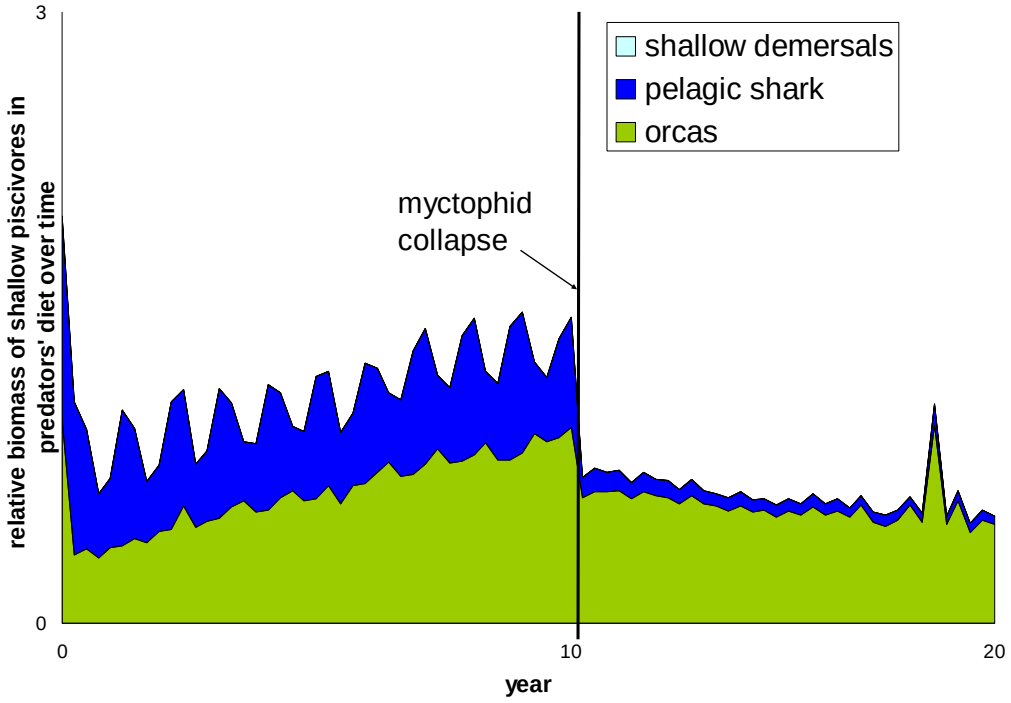

Figure 4-12 Changes in the predation pressure on shallow piscivores with the collapse of myctophids

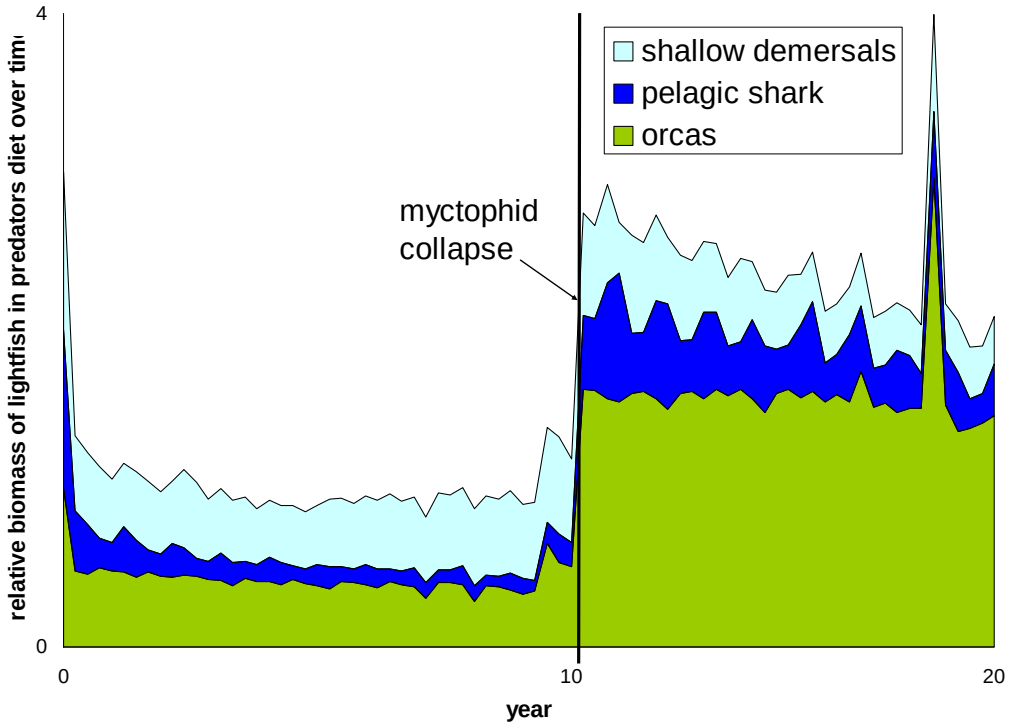

Figure 4-13 Changes in the predation pressure on lightfish with the collapse of myctophids.

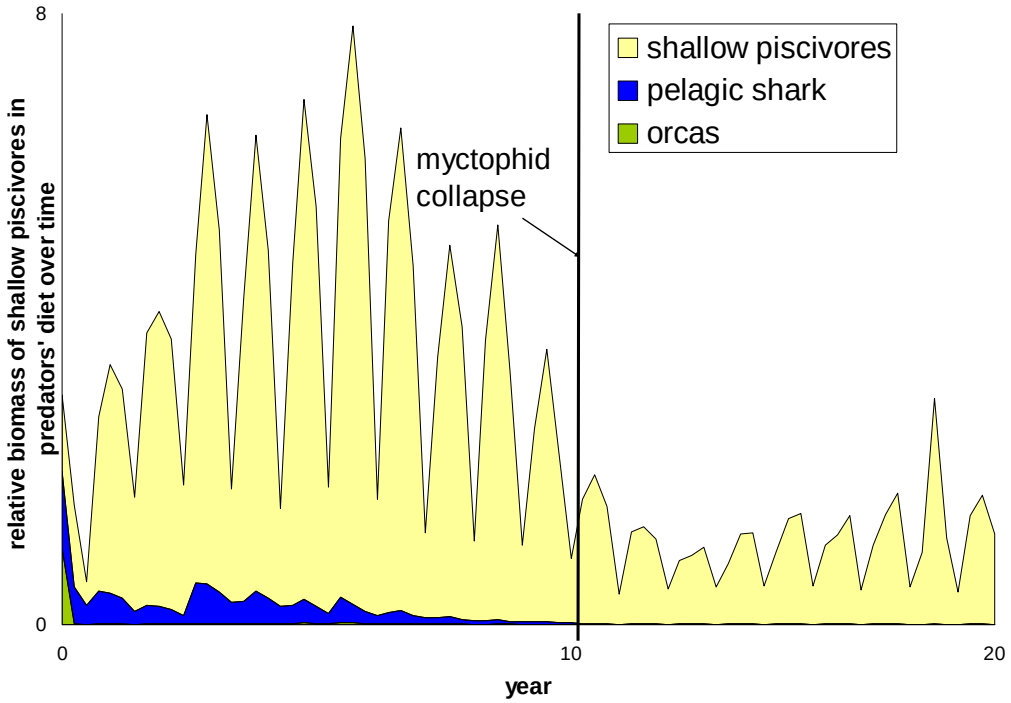

Figure 4-14 Changes in the predation pressure on redbait with the collapse of myctophids.

ASM

Small pelagics

A collapse of small pelagics lead to some impacts in the mid to higher trophic levels of the ecosystem (Figure 4-15). While some groups increased in biomass with the loss of small pelagics (namely mackerel, lightfish and shallow piscivores), the increase was minor, by less than 10% in all cases. The predatory mammals - seals, dolphins and toothed whales - experience a reduction in biomass, but again this was only a small decrease of less than 10%. Small pelagics were only a small portion of the diet of the marine mammals (

Figure 4-16), which explains why only a small impact was seen on these groups with the collapse of the small pelagics. Interestingly, while the shallow demersal fish suffered some increase in predation from the mammals, there was no noticeable impact on their overall biomass.

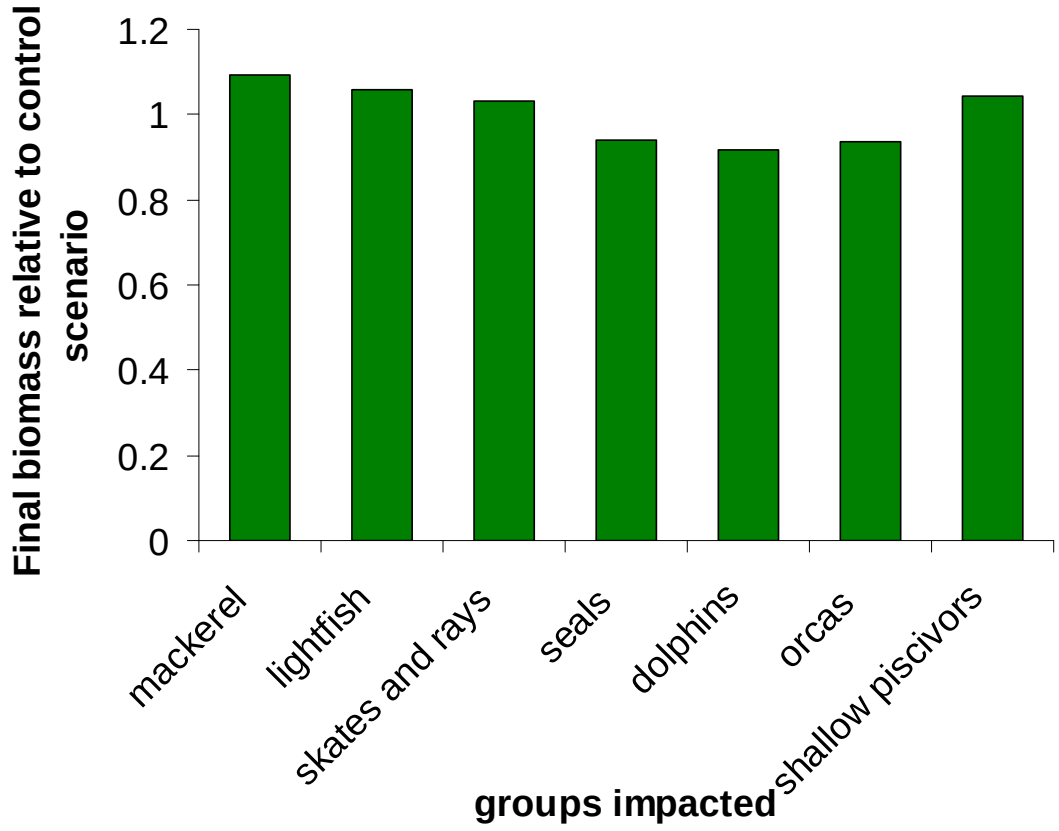

Figure 4-15 Biomass changes resulting from the collapse of small pelagics in ASM

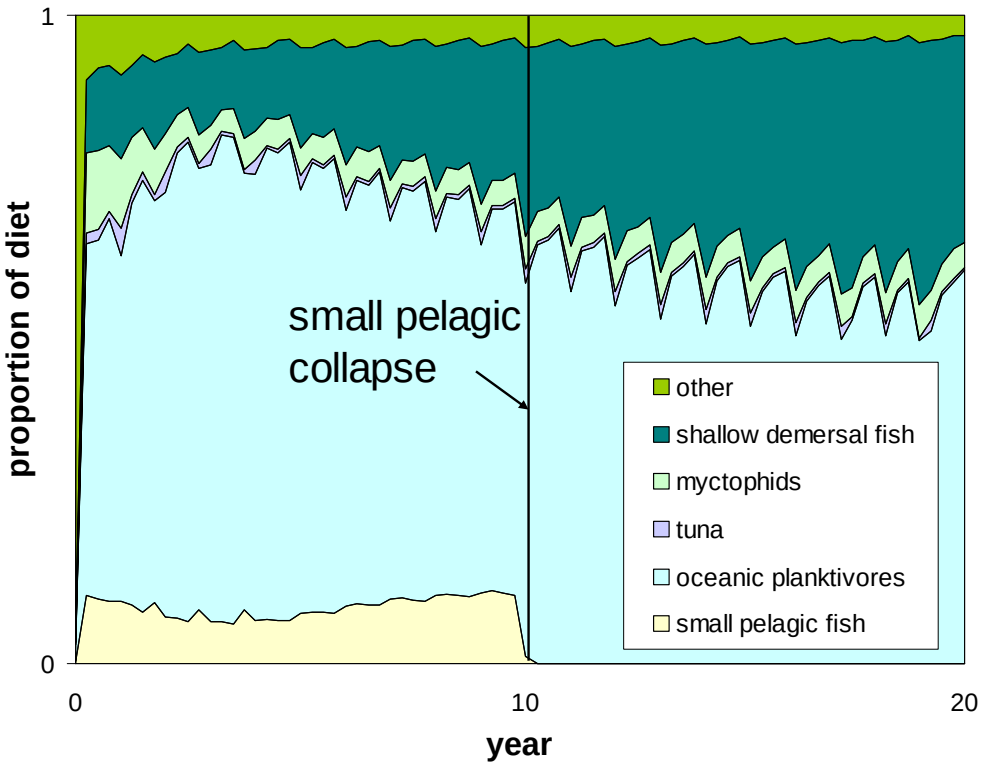

Figure 4-16 Aggregate diet composition of the combined mammal groups with the collapse of small pelagics

Mackerel

The collapse of mackerel had no noticeable impact on the ecosystem in this model. No groups or species varied in biomass from the base case scenario.

Myctophids

As with the small pelagics, the collapse of the myctophids in this model did not have large impacts on ecosystem structure (Figure 4-17). While lightfish, demersal sharks and pinipeds saw a reduction in biomass, it was less than 2% in each case. The reduction in lightfish was due to switching behaviour of groups such as deep demersals with the loss of myctophids as a prey source (Figure 4-18). Deep demersal fish saw a slightly larger reduction, but again, this was only 10%. The larger reduction

in the latter group appears to be because myctophids formed a large portion of their diet.

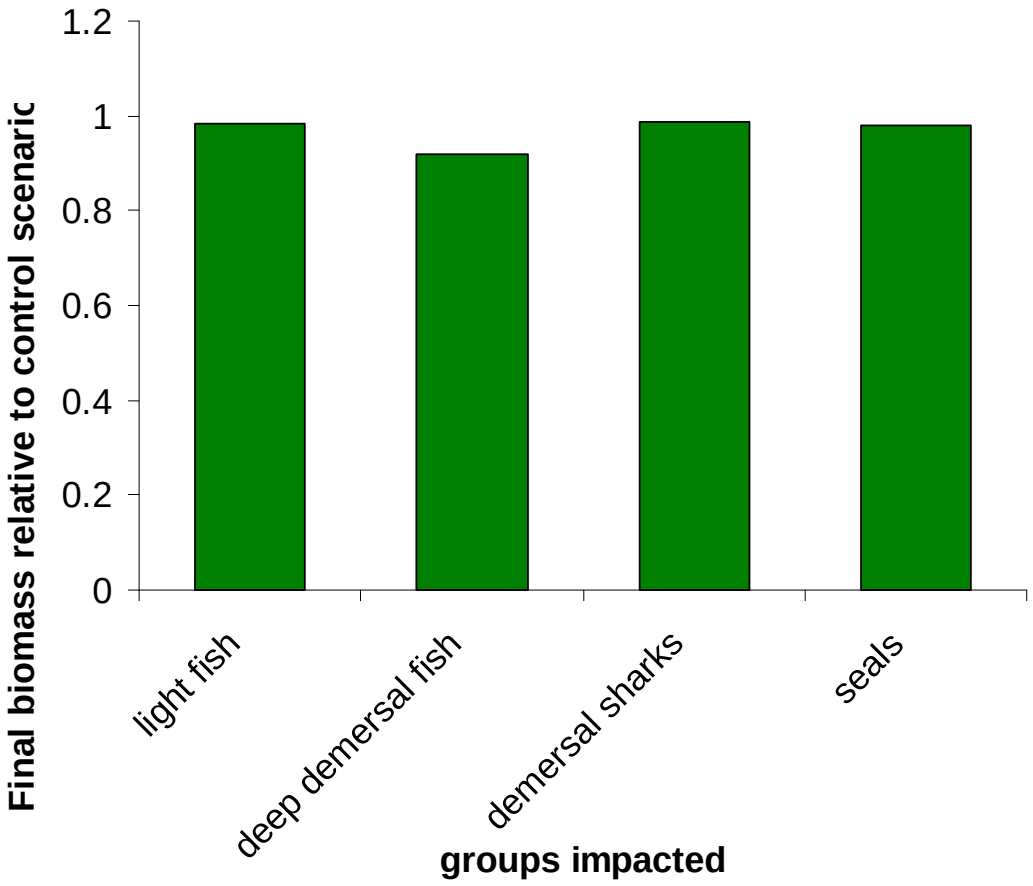

Figure 4-17 Biomass changes resulting from the collapse of myctophids in ASM

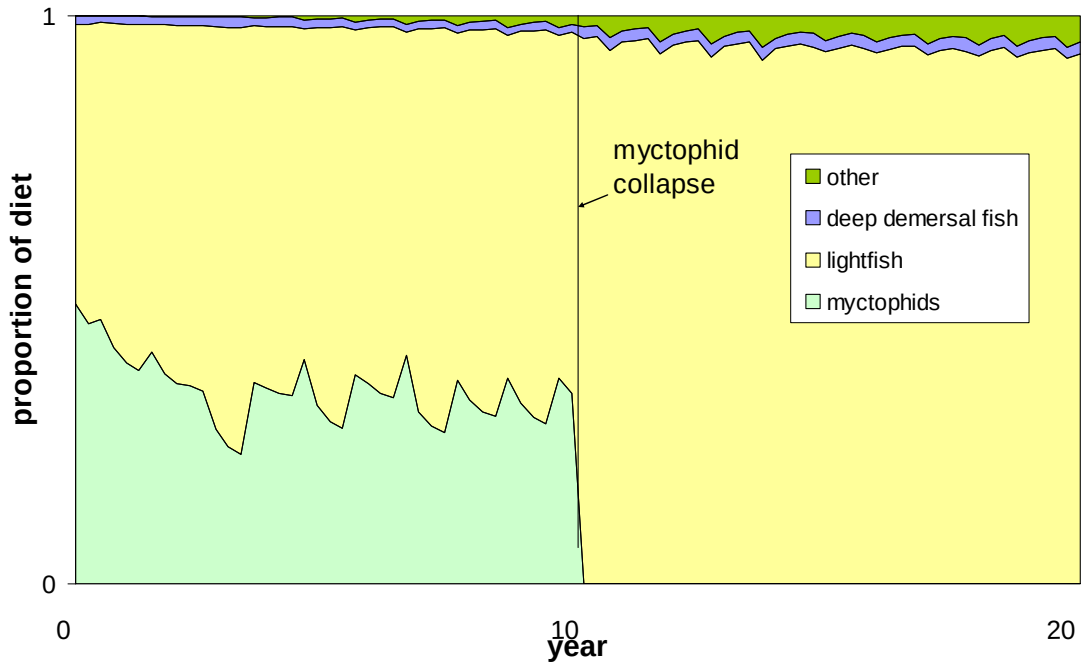

Figure 4-18 Aggregate diet composition of the deep demersal fish with the collapse of myctophids

SETas

Small pelagics and Mackerel

The collapse of small pelagics and mackerel had no noticeable impact on the ecosystem in this model. No groups or species varied in biomass from the base case scenario.

Myctophids

The loss of myctophids from the SETas model has relatively widespread impacts ranging from top predators such as orcas and sharks, down to the zooplankton (Figure 4.18). Tuna, pelagic sharks, seals, orcas and deep demersal fish are all major predators of myctophids in the SETas model, and suffered a reduction in biomass due to a loss of this food source. The small pelagic group suffered a reduction in biomass after the collapse of the myctophid stocks. This was due to the more severe predation pressure from tuna with the loss of myctophids as an alternate prey source (Figure 4-20).

Although the zooplankton shows a slight decrease in biomass, it is not enough to have impacts throughout the foodweb.

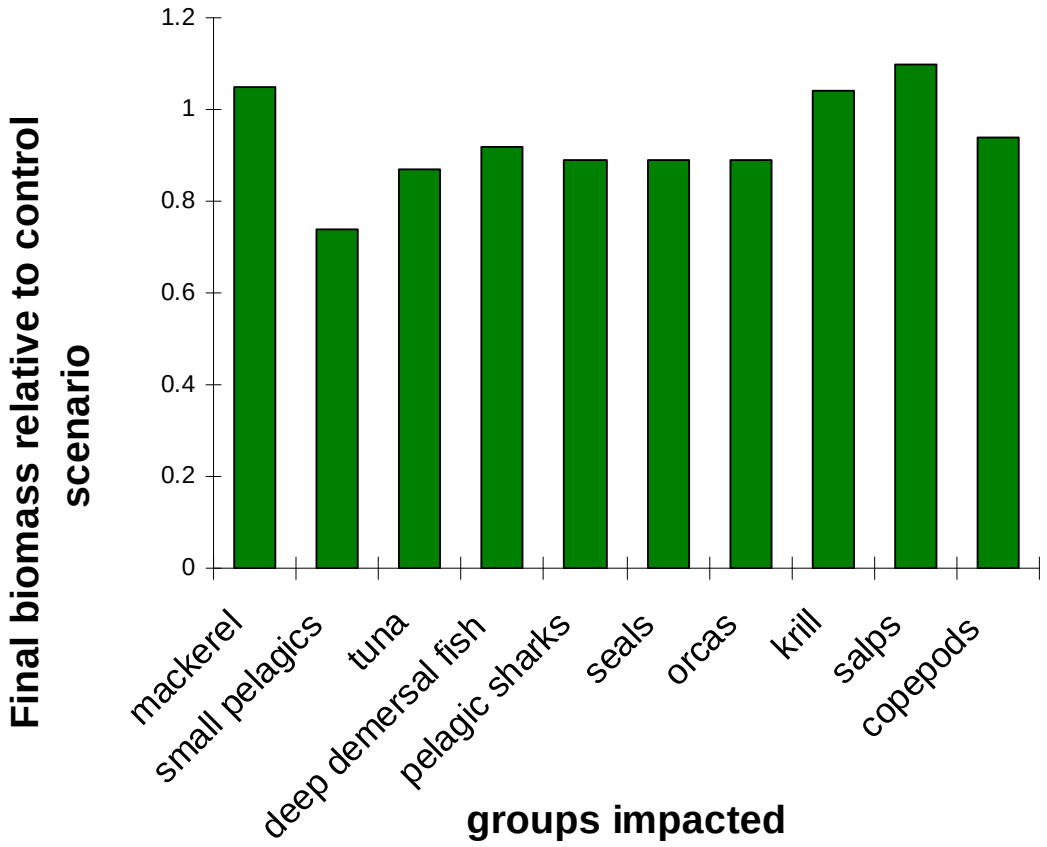

Figure 4-19 Biomass changes resulting from the collapse of myctophids in SETas

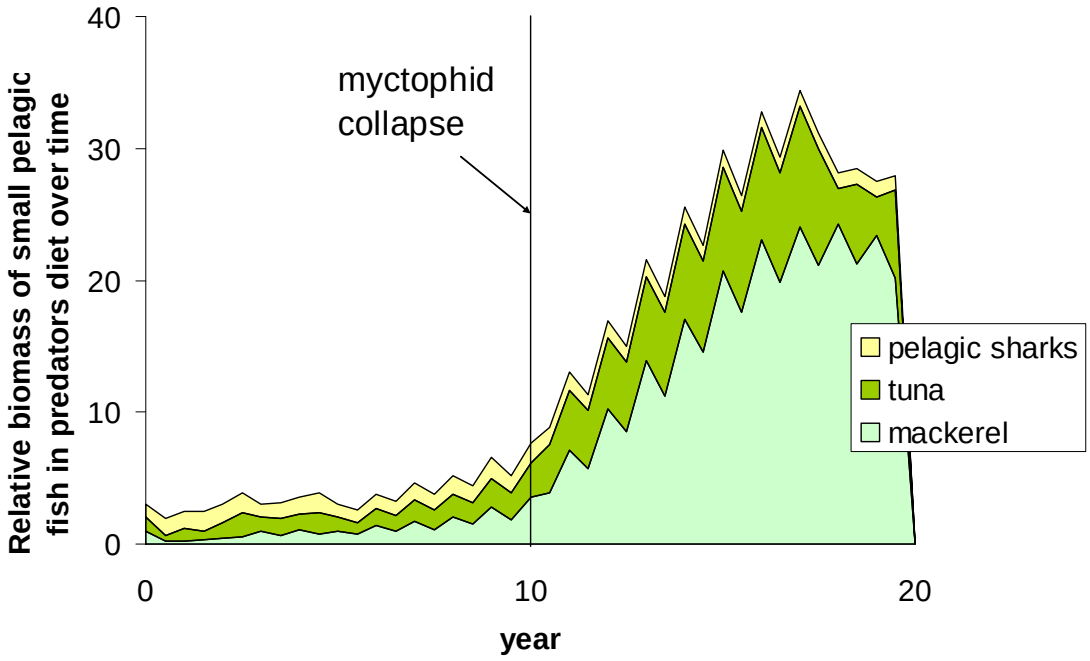

Figure 4-20 Changes in the predation pressure on small pelagic fish with the collapse of myctophids

Discussion

The results presented here highlight the divergent output that can be obtained from models that have been created using different input data, cover different regions, or are created with different purposes in mind. In this way they emphasise the inherent uncertainty that is part of the modelling process. Despite these differences, examination of the output can provide an insight into mechanisms that lead to widespread ecosystem impacts from the removal of a single species or group.

The largest changes in response to these scenarios is in the ASE v2 and the SETas models, when the myctophids are removed. While there are some other small impacts seen in the other models, they are typically minor, and often do not result in obvious changes to the trophic structure. Although in ASE v2 the myctophids represent a higher portion of the overall biomass than they do in ASE v1, they represent a lower overall portion than in the ASM model, where the depletion of the group had much smaller effects. This indicates that while overall biomass may have some impact on the importance of a group in an ecosystem (as is the case of myctophids in the SETas model), there are other drivers that influence how an ecosystem reacts to the loss of a group.

The trophic structure of an ecosystem has been shown to have implications for the function of that ecosystem (Cury et al 2000). Network theory can be used to understand trophic structure in marine ecosystems, and to explain why some species are more likely to cause an ecosystem to become unstable if they are removed. According to network theory, the number of trophic connections that a species has (i.e

the number of other groups that are either predators or prey of that species), dictates how important that species is to ecosystem structure (Gaichas & Francis 2008). Removing a species with many trophic connections is more likely to cause a disintegration of the system, than the removal of peripheral, or less connected species. Thus, removal of species that have a large number of links to other species, leads to a disproportionate impact on the system as a whole, given the biomass of that species. This phenomenon is seen in the runs using ASE v2, where myctophids were very highly connected trophically (all of the piscivores include myctophids in their diet), and the removal of this group lead to both direct and indirect impacts on many other groups in the system.

While network theory goes some way to explain the potential for a species or group to be a keystone of the system, it does not fully explain the results obtained here. While the connectedness (the number of trophic links) is the same in the two versions of the ASE model, very different results are obtained. These results indicate that it is the strength of the connections - in addition to the number of connections - that contributes to the importance of a particular group in the ecosystem. For instance, while small pelagics are highly connected in ASE v2, the strength of the connections is universally weak (i.e. they only represent a small portion of any other species' diet), resulting in very little impact when this group is removed. Myctophids have a similar level of connectivity to small pelagics, but in ASE v2 the strength of the links is much greater, and a correspondingly high impact is seen with the removal of myctophids. These findings agree with those of Travers et al (2009), who found that the proportion of a particular group in the diets of the other groups in the system is an important

factor in whether the removal of that group will have an impact throughout the ecosystem.

While ASE v2 did see some large impacts, it must be remembered that this version of the model was parameterised specifically to create an ecosystem with a high proportion of the piscivores diets made up of myctophids[2]. The collapse of myctophids therefore causes dietary shifts in many of the piscivorous and planktivorous groups (juvenile myctophids are small enough to be consumed by planktivores). Recent work by Kloser et al. (2009) has indicated that the proportion of mesopelagics in this system may indeed be as high as was represented by the ASE v2 model (roughly an order of magnitude higher than in v1). This suggests that the shifts in the ecosystem seen in ASE v2 may be representative of plausible impacts if mesopelagics were heavily fished. Interestingly, the collapse of myctophids in ASEv2 causes an asymmetric ecosystem impact, where predators are impacted but not prey species. This highlights that while a species may not be the critical link in a typical 'wasp-waisted' system, it may still be a major food source and therefore a key species for the structure and function of the ecosystem.

Comparing across models, it is apparent that the existence of alternative, equally strong, trophic pathways can also affect model dynamics. For instance, although myctophids contribute to the diet of many groups in the ASM model, they do not have the same ecosystem impact as they do in ASE v2. This is because there are other

[2] While both models are consistent with the data available at the time of their development that data was highly uncertain (as evidenced by the order of magnitude differences in estimates of myctophids used in the two model variants). ASE v1 used trophic connections more heavily weighted toward "light-moderately connected" interpretations of the available diet data, whereas v2 used connections more heavily weighted to "strong connections and high prey availability".

groups in the ASM model that are also important prey groups for the predatory groups (eg, small pelagics, squid, trevalla, demersal fish). So, while myctophids are one of the few groups with strong trophic links to many other groups in ASE v2, in ASM there are many groups with the same strength and number of connections. In ASM the high interconnectedness of the entire system means that there are multiple trophic pathways existing, which make it possible for other groups to fill the niche that is left when myctophids are removed.

In addition to connectedness and biomass, a third factor that appears to be driving these results is the spatial complexity of the model domain. Spatially complex models have been shown to prevent extinction (Keitt 1997) and competitive exclusion (Hassell et al. 1994) by providing more refugia than spatially simple models (Fulton et al. 2004c). It is clear from the divergent results between the most spatially simple model, SETas (with 10 boxes) and the most complex, ASM (with 80 boxes) that the spatial complexity plays a part in determining its behaviour in these scenarios. A notable difference between these models is the different groups that were impacted from the collapse of myctophids. In the SETas model, all zooplankton groups were impacted from the loss of myctophids, whereas in the ASM none of these groups were impacted. This change was fundamental in effecting the other impacts seen in these models. Although this is obviously an artefact of the modelling rather than an ecosystem dynamic, it nevertheless needs to be born in mind when analysing modelled ecosystem impacts, or indeed in the initial phase of the model development.

Conclusions

Ecosystems structured in different ways will require different fisheries management strategies in order to achieve a sustainable fishery. Therefore the trophic structure of the system needs to be determined, in terms of both the connectivity and the strength of linkages between species. While work has been done on this issue (eg, Bulman et al 2001, Bulman et al 2002), confounding factors make it difficult to create a comprehensive and accurate picture of the trophic structure. For instance, the trophic structure in many systems may be dynamic, with predators being opportunistic, depending on the densities of various prey species. Indeed, recent work suggests that there have been major changes in the community composition, distribution and diets of fish in the North Sea over the past 100 years (Pinnegar 2010). Therefore one static parameterisation may not capture changing system complexities.

By gaining a comprehensive understanding of both the strength of trophic connections and the relative biomasses of different species, we are better able to determine what the impact of high levels of fishing pressure will be on the overall ecosystem. However, temporal and spatial variability in relative biomasses may have further impacts and consequences that have not been explored in this work.

It is difficult to predict whether any species will behave as a keystone in south eastern Australian waters. More comprehensive data on trophic connections and the strength of these connections throughout the system would increase the likelihood of making

an accurate prediction regarding a collapse in any of these lower trophic level fish groups. This study reinforces the need to continue to collect information about the trophic structure and function of Australia's marine ecosystems to underpin ecosystem based fisheries management.

Chapter 5. Using a telescoping approach to model ecosystem impacts of the implementation of Marine Protected Areas

Abstract

As fish stocks are becoming increasingly vulnerable to overfishing and collapse, Marine Protected Areas (MPAs) are seeing increased utilisation, both to conserve ecosystems and to replenish fish stocks. There remains however, some controversy as to how effective MPAs are both as a tool for conservation and for providing increased yield outside of the closed area. One of the main factors that appears to impact how effective an MPA will be in modelled ecosystems is the level of movement of organisms, both in the larval stages and as adults. When using modelled systems to explore the effectiveness of MPAs it is therefore imperative to give consideration to the movement of the biotic components and the spatial structure of the model through which these components can move. In this chapter three simple alternative management techniques are explored: MPAs with displaced fishing effort; MPAs without displaced fishing effort (i.e. a reduction in overall catch); and no MPAs imposed. To provide a more detailed representation of fish movement, which is a key process to incorporate in the analysis, a telescoping approach is used to represent a fine scale spatial structure around the closed areas. The results indicate that while MPAs can provide protection for ecosystems within the closed areas, protection does not necessarily extend beyond the closures, nor translate into increased fisheries yield.

Introduction

The protection of biodiversity, habitat and fishery stocks in our oceans has become a fundamental concern for management in a time when many fish stocks are in decline, and biodiversity and habitats are seriously threatened (Worm et al. 2006). This has lead managers to re-consider traditional management techniques, and seen the interest in spatial management, in particular Marine Protected Areas (MPAs) grow. MPAs are now often seen as a crucial step towards the implementation of ecosystem-based management (Browman & Stergiou 2004, Douvere & Ehler 2008), to address both conservation and fisheries objectives. However, the benefits of MPAs to both conservation and fisheries is equivocal; some MPAs appear to be effective in protecting biodiversity and increasing biomass, whilst others do not (Halpern 2003). Although some species have been shown to benefit from the protection from fishing inside MPAs (e.g. lobsters in Tasmanian MPAs (Edgar & Barrett 1999), indirect effects of trophic cascades may cause the opposite effect for other species. This can potentially lead to a loss of biodiversity for the system as a whole (Savina et al. 2009). Worm et al. (2006) for example, found that species richness decreased in 21% of 43 study sites, inside protected areas throughout the world. Furthermore, of the ten most detailed studies (in terms of sample size), half showed a decrease in species richness. It is clear that the introduction of MPAs will not necessarily increase biodiversity within the entire system, or even within the MPA itself. It is therefore imperative that further work be done to understand the ecosystem dynamics that influence the success or otherwise of MPAs. It is clearly not the case that simply closing off one section of the marine environment will necessarily allow it to revert to a pristine state. Although empirical data collection both inside and outside of an MPA allows us to assess the relative biology in both regions, it does not typically explain why these differences

occur (exceptions being where processes have been tracked along with trends, but this is exceptionally rare). Moreover, empirical data is often difficult and time consuming to acquire in regards to the biological impacts of MPAs, making it problematic to assess whether the closures are indeed meeting the conservation and fisheries goals.

Ecosystem models have developed to the point where they can represent complex ecosystems, from nutrients up to top predators. Although models of marine reserves are relatively new in the scientific literature, they are becoming more frequent and there is now a significant body of work examining how models can help with the implementation and understanding of marine reserves. Two major findings that have emerged from these studies are; movement of larvae and adult fish and invertebrates is a factor in determining how protected they will be from an MPA; and indirect trophic effects have the potential to influence both conservation and fisheries impacts of the MPAs (Gerber et al. 2003, Botsford et al. 2009, Savina et al. 2009).

Marine dynamics are complex because of the variable degrees of movement seen in larvae, fish, invertebrate and fishers, as well as in the abiotic components of the marine system (Botsford et al. 2009). The high degree of connectivity within the ocean environment makes it unlikely that we can gain a thorough understanding of the impacts of an MPA by only focusing on the protected area and the area immediately surrounding it. Indeed, the very act of closing an area to fishing may have impacts on the surrounding area through the displacement of fishing effort that often occurs. Thus, ecological impacts and fisheries impacts from the closed area can traverse a much broader scale than the MPA itself. We therefore need to understand what the

impacts are across a broader region if we are to comprehensively assess the impact of an MPA. In order to do this we need large scale spatial models.

As well representing the spatial complexity of an area, to effectively capture the impacts of an MPA, complex trophic dynamics must also be incorporated. Indirect effects are often very difficult to measure empirically or to predict. One of the strengths of ecosystem models is the ability to allow complex biological dynamics to play out under a range of management scenarios, in order to gain an understanding of potential indirect impacts. To take advantage of this strength, multispecies models must be employed that can represent trophic interactions that may occur when fishing is removed from specific spatial zones within a system.

The overall aim of this work is to examine the hypothesis that the ecosystem benefits of MPAs remain when there is no loss of yield to fisheries (i.e. fishing effort is displaced into the surrounding non-protected areas). This is tested through model simulations of fishing and MPAs in south-eastern Australia and comparing MPAs with and without displaced fishing effort, using a range of ecological indicators.

By their very nature, models must be a simplification of the real world, and it is the task of the modeller to determine the components that must be incorporated into the model to ensure a realistic representation of the scenarios that are being questioned. The approach used here to investigate MPAs focuses on representing two critical components of marine ecosystems that influence the performance of MPAs; biological movement and trophic interactions. This study utilised a spatially explicit model, with a 3 dimensional, finely detailed box model structure that includes sub-

box scale habitat patchiness to resolve fish distribution and movement. Secondly, a multispecies approach is taken to take into account potential indirect effects caused by trophic interactions between species.

Methods

Model structure

The model used in these scenarios is the Atlantis Spatial Management (ASM) model. The ASM model uses the Atlantis ecosystem modelling framework (Fulton et al. 2004b, Fulton et al. 2011). The biophysical sub-model of Atlantis tracks nutrient flows through the main biological and detritus groups within marine ecosystems. Processes such as production, consumption and growth, habitat dependency, reproduction, movement and large-scale migration, predation and other forms of mortality and waste production are all handled explicitly. The trophic resolution is typically at the functional group level, although some age-structured single species groups are also included. The outputs of the model consist of deterministic time series for each biological component in each spatial cell in the modelled ecosystem. A full description of the parameterisation and structure of this model can be found in Johnson et al. (2011) (included in this volume as chapter 3).

Model scenarios

Three alternate scenarios were modelled in this study. The first (scenario 1) included a low level of fishing across the entire model domain, with no closure or fishing restrictions at all. Scenario 2 involved the application of large protected areas across

the model domain, effectively closing off roughly a third of the coastal areas (Figure 5-1), and reducing overall fishing levels so that the non protected areas were under the same levels of fishing pressure as applied to those boxes in scenario 1. This had the effect of reducing the overall catch as there was no effort displacement. In scenario 3 the same areas were closed to fishing as scenario 2, however scenario 3 imposed a higher catch rate in the non-protected areas; this meant the overall yearly catch across the model was almost identical to the catch obtained in scenario 1 (the largest deviation of catch between scenarios 1 and 3 was 0.5% per group, with most groups showing 0-0.001% deviation), but this was achieved by concentrating fishing pressure in unprotected boxes (i.e. effort was displaced).

In all scenarios, the model was run for 10 years as a burn in period and then another 10 years under the imposed scenario conditions. There was no fishing in the burn in periods in any run, so that both the fishing pressure and the protected areas were imposed at year 10 in all cases.

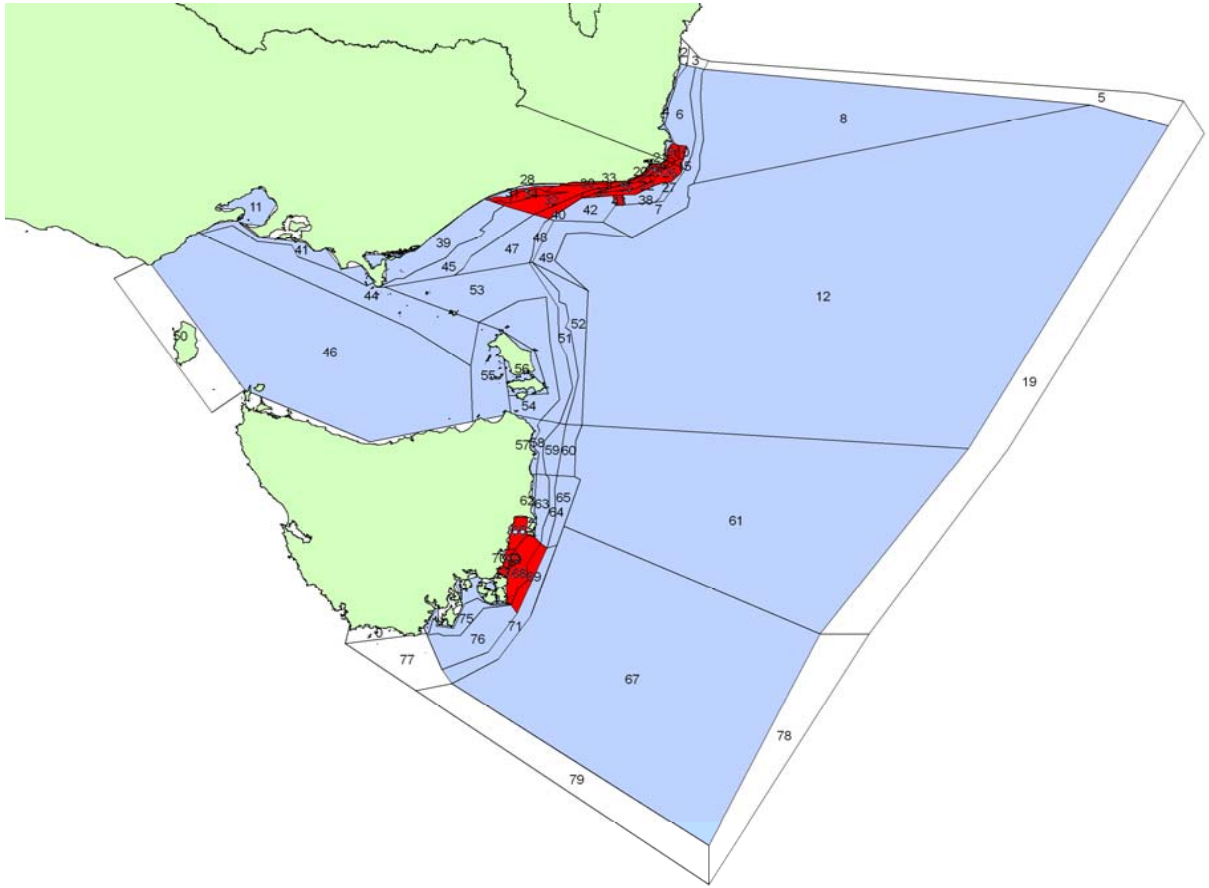

Figure 5-1 Model domain with fishing closures imposed in scenario 2 shown in red.

Indicators

The indicators used in this study were drawn from Fulton et al (2004a), Fulton et al (2007) and Link (2005). Indicators were chosen that could be feasibly calculated and tested in the ASM model, and cover the primary indicators used to date to monitor MPAs. The complete set of indicators tested are listed in Table 5-1 and include the following broad types: relative biomass, structural, industry and socioeconomic. While biodiversity is also an important indicator when monitoring real ecosystem, in ecosystem models where species are aggregated to form functional groups, and complete extirpation is difficult, it is very difficult accurately represent biodiversity. One method that has been used for ecosystems models is Kempton's index (Kempton & Taylor 1976). The index describes the slope of the cumulative species log abundance curve between the lowest and the highest quartiles, expressed as;

$$Q = 0.5S / \log(B_{0.25S} / B_{0.75S})$$

where S is the number of functional groups (with a trophic level of three or more) and B_{xS} is the total biomass of the xS most abundant groups (Kempton & Taylor 1976). It is dependent on relative biomasses of species or groups and so is well suited to simulations in which the number of groups may not change (Ainsworth & Pitcher 2006). The Kempton's index is used here as a way to measure the biodiversity of the system.

Table 5-1 Indicator types and indicators measured in this study

Indicator type	**Indicator**
Structural	habitat cover
	pelagic:demersal ratio
	planktivore:pisvicore ratio
	infauna/epifauna
	average vertebrate trophic level
	biodiversity (Kempton's Q)
Relative biomass of species or groups	biomass of habitat associated (reef) fish
	biomass of demersal fish
	biomass of zooplankton
	biomass of top predators
	biomass of gelatinous zooplankton
	biomass of piscivores
	biomass of pelagic shark
	biomass of small pelagic planktivores
	biomass of scavengers
	biomass of cephalopods
	biomass of lobster
	biomass of blue throat wrasse
	biomass of purple wrasse
	biomass of pink snapper
	biomass of magpie perch
	biomass of banded morwong
	biomass of silver sweep
	biomass of zebra fish
	biomass of abalone
	biomass of dogshark
	biomass of dogfish
	biomass of pelagic shark
	biomass of demersal shark
	biomass of mackerel
	biomass of shallow demersal reef fish
	biomass of seagrass
	total biomass
Industry	biomass of commercial species
	total yield
	total value
Socioeconomic	biomass of charismatic species

Results

Impacts across the whole modelled area

Generally there is a more pronounced difference seen between scenario 1 and 2 than there is between scenario 1 and 3. When there is no change in the per km fishing pressure outside the closed area, there is a more dramatic change to the ecosystem than there is when there is an increase in the fishing pressure across the domain.

Looking at specific indicators there are contrasting results for the different functional groups and indicators examined here, some showing an increase and other showing a decrease (Figure 5-2 and Figure 5-3). In these results the changes in the system are not defined as either positive or negative, as such a judgement is dependant on the goals and criteria of interest. For example, there is an increase in the biomass of abalone in both scenario 2 and 3, which is generally considered an improvement due to the high commercial value of this species. However, given that it occupies a low trophic level, this increase in biomass also translates to a lower average trophic level of the system, which is generally considered a negative impact in terms of ecosystem structure (although in this case the difference in average trophic level is negligible). For the same reason, the increase in biomass of planktivorous fish is often considered a deterioration of system state. However, if this is simply a case of increased biomass as a result of reduced fishing pressure, with no associated ecosystem impacts, it is uncertain whether this should indeed be considered a negative impact on the system in this context.

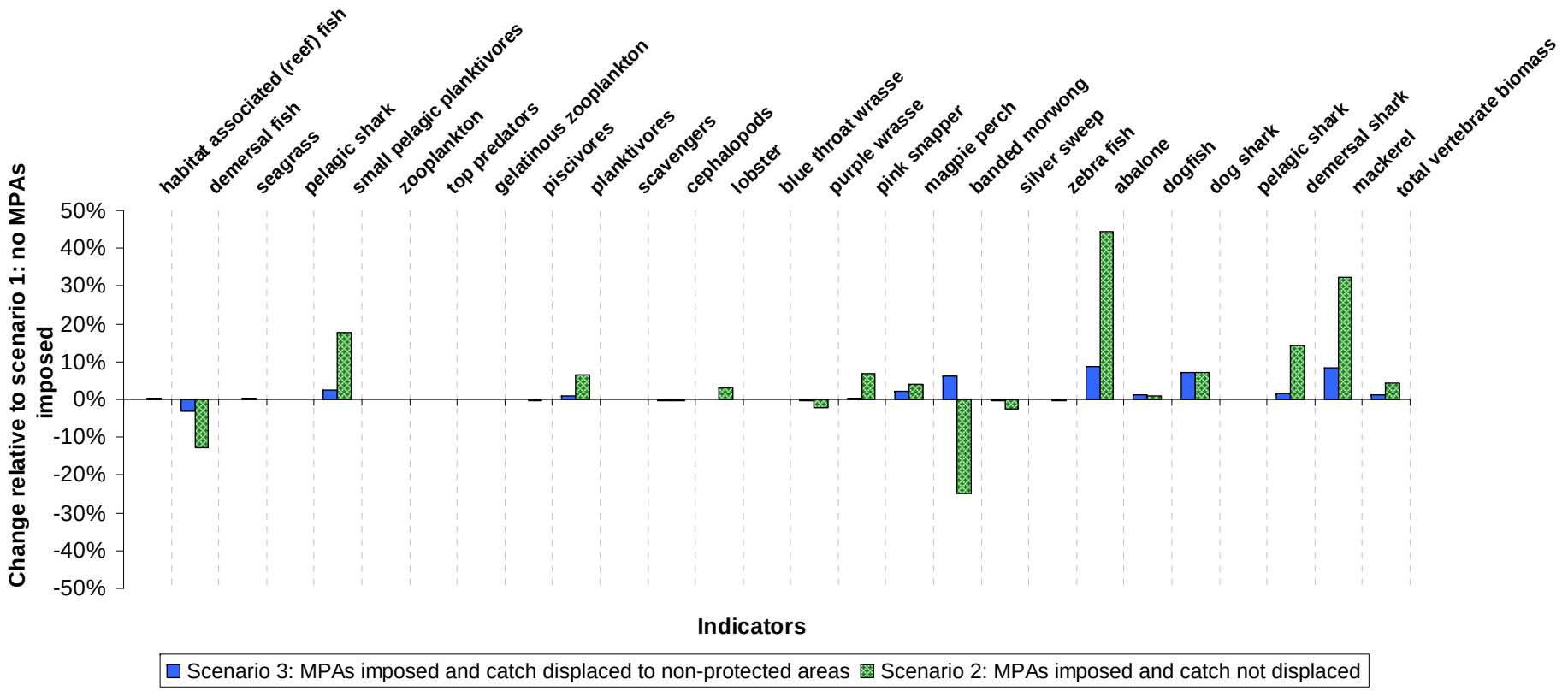

Figure 5-2: Changes to the biomasses of individual groups across the entire domain in scenario 2 and scenario 3 relative to scenario 1.

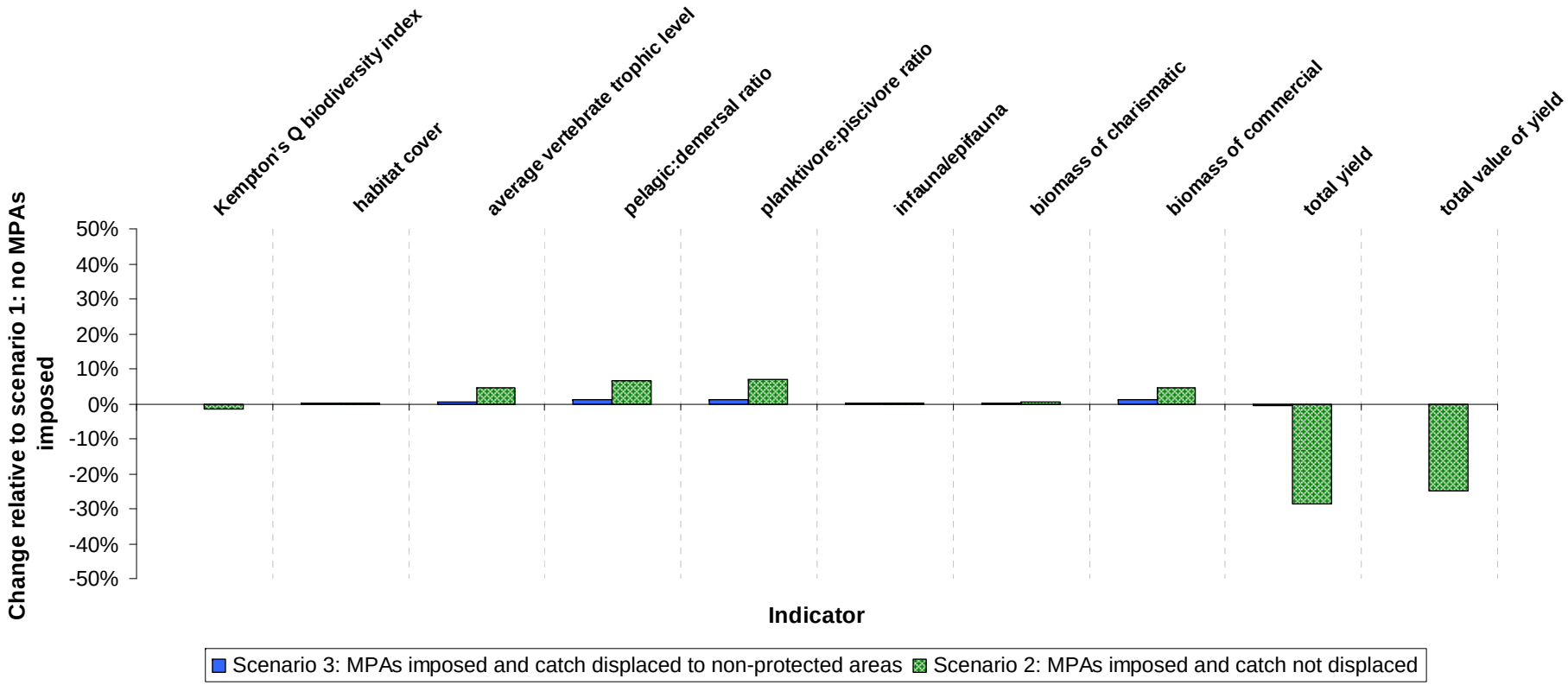

Figure 5-3: Changes to the structural and industry indicators across the entire domain in scenario 2 and scenario 3 relative to scenario 1

The biomass of banded morwong showed the most marked difference between the comparisons of scenario 1 with scenario 2 and 3. This group increased by 6.28% in scenario 3 whereas in scenario 2 the biomass decreased by 24.48% (Figure 5-2). In addition, the age structure of this group changes substantially by the end of the 10 year scenario projections. When there was no MPA imposed (scenario 1), the oldest age classes were nearly completely fished out, leaving the majority of the population as small, younger age classes. In longer runs that were done, this trend continues so that the populations continues to decline, eventually leading to a recruitment failure as all the breeding age classes are removed. When the MPA is imposed (regardless of the magnitude of off reserve fishing pressure), there is a sharp difference in the age structure, with a higher proportion of the population falling in the older age classes (see the results for scenarios 2 and 3 in Figure 5-4). However, despite this increase in the ratio of older age classes in scenario 2, there is still an overall decline in biomass; the result of an increase in predation by the demersal shark group (which increases in biomass by 14.22% in this scenario).

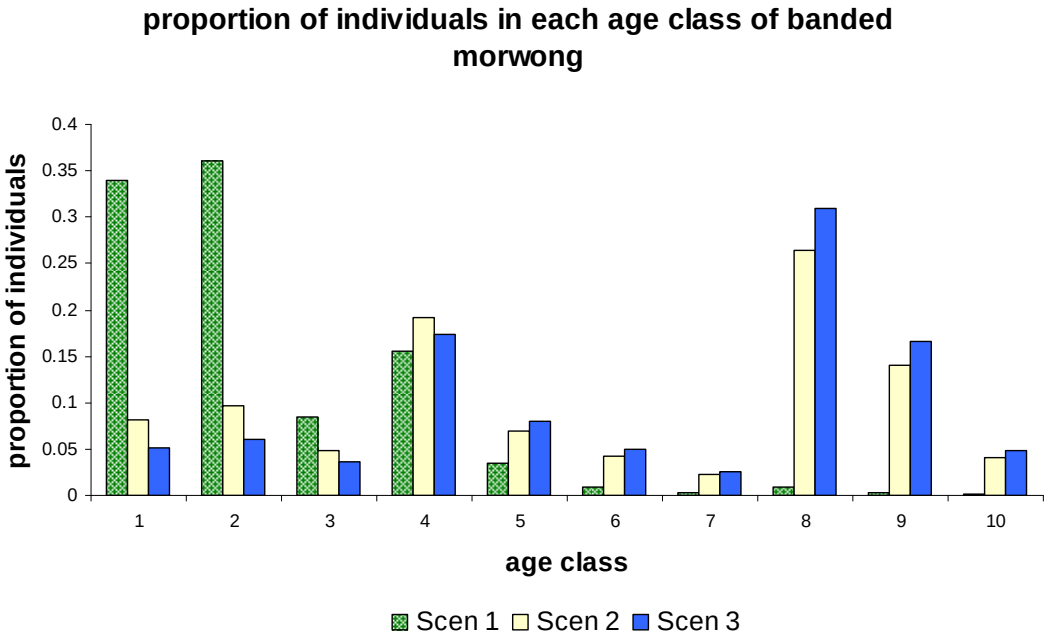

Figure 5-4: Age structure of banded morwong under the two scenarios

In contrast to the morwong, abalone biomass increased with the introduction of MPAs, more so when catch was not simply displaced onto unprotected areas. The biomass of abalone increased by 8.6% in scenario 3 and rose 44.42% in scenario 2. The sedentary nature of abalone meant that the MPAs consistently provided protection for this group, but this increase in biomass inside the protected areas did not translate to an increase in biomass outside of the MPAs. The higher standing biomass of abalone in scenario 2 compared to scenario 3 is a direct result of the reduced catch of abalone in scenario 2 (displaced catch in scenario 3 drawing down unprotected stocks, compensating at a system level for the increases allowed within the protected area). There was some change to the age structure of abalone between the three scenarios, with a slight increase in the proportion of older age classes in scenario 3, and a greater increase in scenario 2 (Figure 5-5).

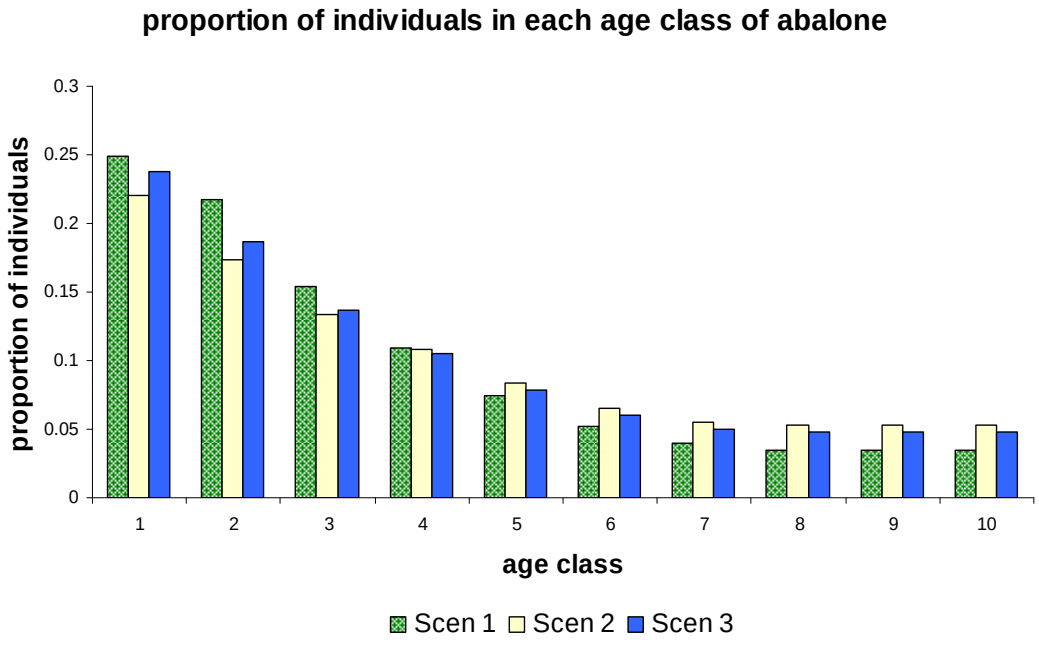

Figure 5-5: Age structure of Abalone under the two scenarios.

The biomass of dogshark increased by a similar degree in scenario 2 (7.02%) and scenario 3 (7.08%). The age structure of dogshark also sees an increase in the older age classes with the MPAs in place (i.e. in both scenarios 2 and 3), resulting in a relatively even distribution across all age classes as opposed to the higher proportion of juvenile dogshark in scenario 1 (Figure 5-6).

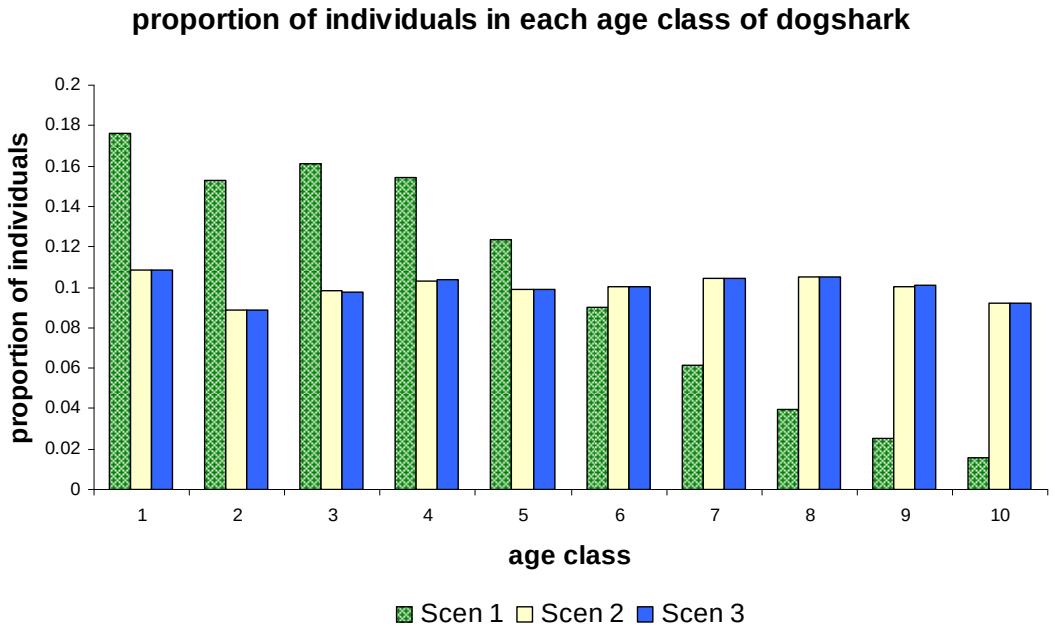

Figure 5-6: Age structure of dog shark in the two scenarios

The biomass of mackerel also sees a slight increase with the introduction of the MPAs. The age structure of mackerel does not change as much as does the dogfish and banded morwong structure, however an increase in the older age classes is still apparent in this group when the MPAs are imposed in both scenarios 2 and 3. The higher biomass of mackerel seen in scenario 2 compared with scenario 3 is due to the higher catch of this group under scenario 3, which leads to slightly lower numbers in the older age classes (Figure 5-7).

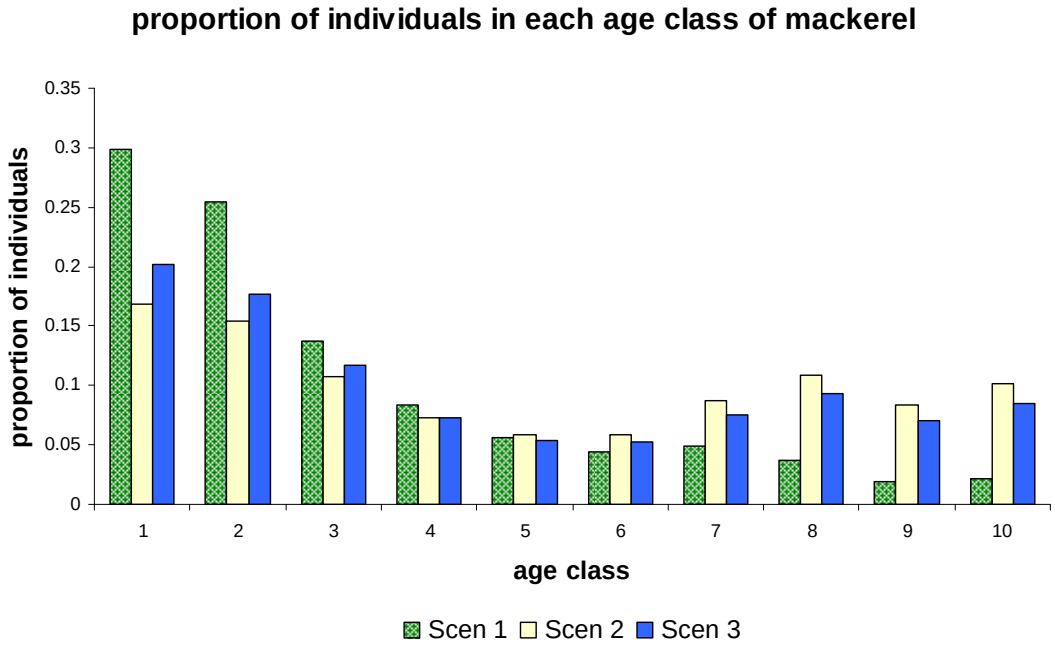

Figure 5-7 Age structure of mackerel in the two scenarios

Socioeconomic objectives must be considered along with ecological indicators. Looking at the fisheries implications of the management actions, the total yield and total value of yield showed only negligible differences between scenarios 1 and 3, as they were specifically parameterised so that the entire effort from inside the MPAs was displaced in scenario 3. In scenario 2 there is a drop of approximately 29% in the biomass of yield and a drop of 25% in the total value of the yield when fishing pressure is not displaced.

Results from inside the MPAs

The indicators that were used to measure overall system state were also used to explore the state of the ecosystem inside the area that was subjected to closures in scenario 2 and 3. Figure 5-8 and Figure 5-9 show the results of each indicator are the end of the 10 year projections, but only calculated for those boxes wholly within the MPAs.

There are much greater differences seen between inside and outside the MPAs in scenario 3 than there are in scenario 2. There is a significant increase in biomass over the 10 years (i.e. from the end of the burn in period to the end of the scenario projection) for many of the groups inside the MPAs in scenario 3; small planktivores show an increase of 13%, magpie perch increases by 10%, banded morwong shows the greatest increase of 181%, abalone increases by 12%, dogshark 5%, dogfish 11% and mackerel by 31%.

There is a similar increase in biomass of many groups inside the MPAs in scenario 2, however this increase is more in line with the increases across the entire domain (Figure 5.2). In this scenario the groups that undergo a substantial increase in biomass inside the MPAs are; small planktivores (increase by 30%), pink snapper (up by 8%), banded morwong (rising by 104%), abalone (45% higher), dogshark (increasing by 5%), dogfish (increasing 11%), demersal shark (rising 13%) and mackerel (up by 57%) (Figure 5.8).

The increase in the biomass of banded morwong is also significant in both scenarios inside the MPAs. Whereas the overall biomass of banded morwong decreased overall in scenario 2, due to predation by demersal shark, the population inside the MPA increased twofold, due to the provision of protection from fishing for this species within the MPA. This refuge was even more pronounced in scenario 3 where there was very little increase in the biomass of demersal sharks to offset the increase in banded morwong biomass.

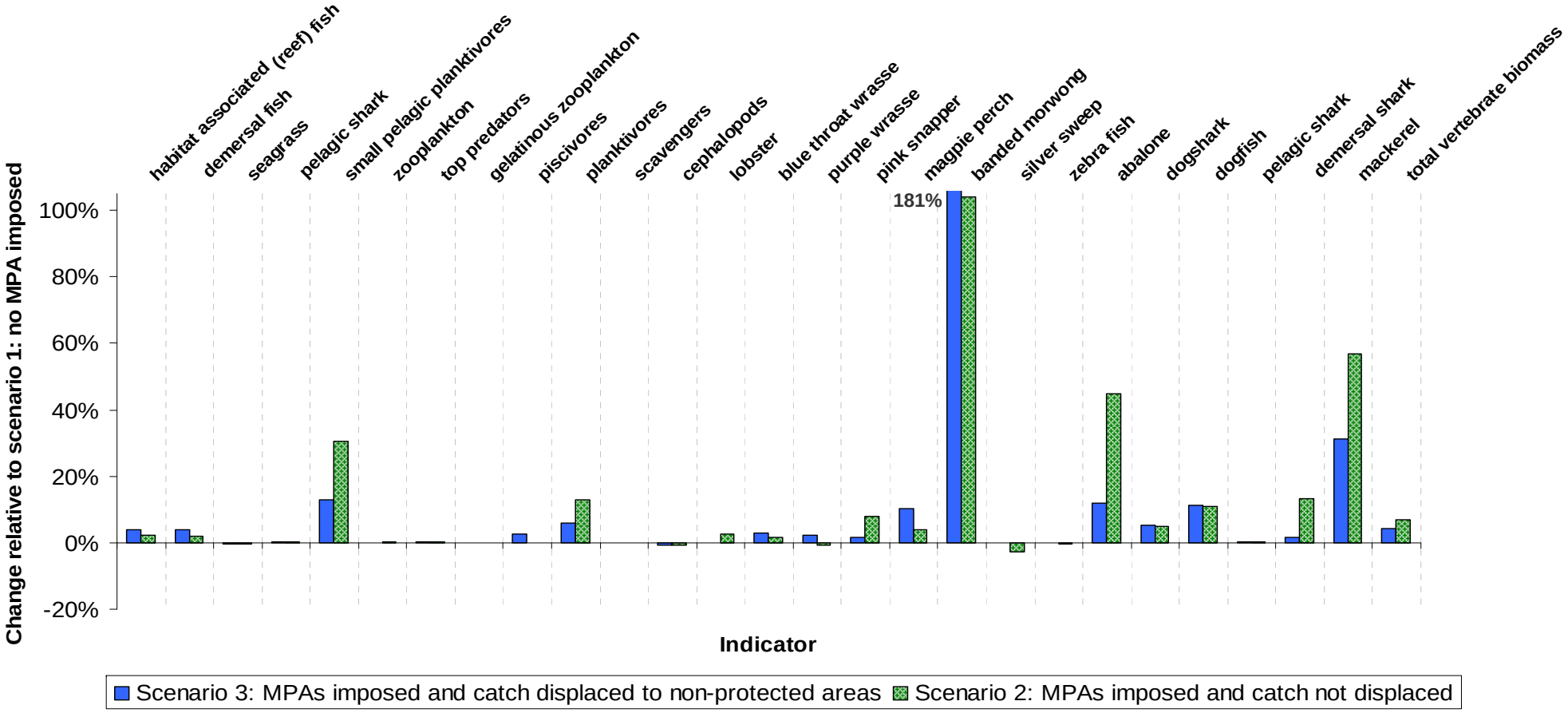

Figure 5-8: Changes to the biomasses of individual groups inside the MPA in scenario 2 and scenario 3

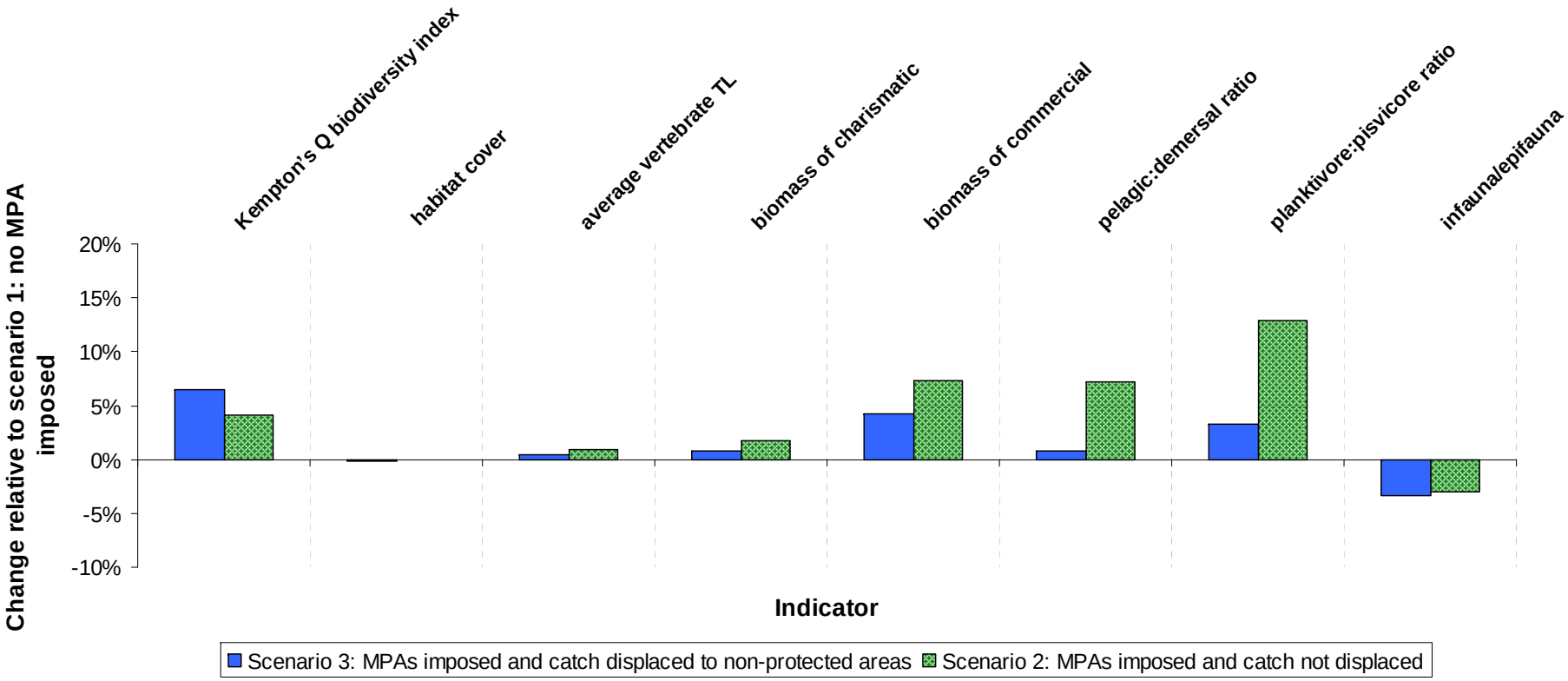

Figure 5-9: Changes to the structural indicators inside the MPA in scenario 2 and scenario 3

A notable difference between the results from inside the MPA and the entire domain results is that there is an increase in the biodiversity index inside the MPAs in both scenarios with MPAs imposed, compared with scenario 1, with no MPA (i.e. the signal in the diversity index is scale dependent). This increase is larger in scenario 3 where the catch is displaced to areas outside the reserve (6%), compared with when there is no displacement (4%). This is in contrast to the change in biomass of vertebrates inside the MPAs. There is a larger increase in vertebrate biomass in scenario 2 (7%) in comparison to scenario 3 (4%).

All of the structural indicators increased inside the MPAs in both scenarios, except the infauna/epifauna ratio, which showed a slight decrease. There was some difference between the two scenarios however. The biomass of charismatic and commercial species both increased substantially more in scenario 2 (2% and 7% respectively) than in scenario 3 (1% and 4% respectively). Similarly, the pelagic/demersal ratio and the planktivore/piscivores ratio also increases more in scenario 2 (7% and 13%) than in scenario 3 (1% and 3%).

Comparison of inside and outside MPA

The most obvious difference between the indicators inside and outside the MPAs is the large increase in banded morwong inside the MPAs compared with outside (129% in scenario 2 and 175% in scenario 3). The second largest difference is the biomass of mackerel which also increases inside the MPA compared with outside in both scenarios. Demersal fish and small planktivorous fish also see moderate increases inside the MPAs in both scenarios (Figure 5-10).

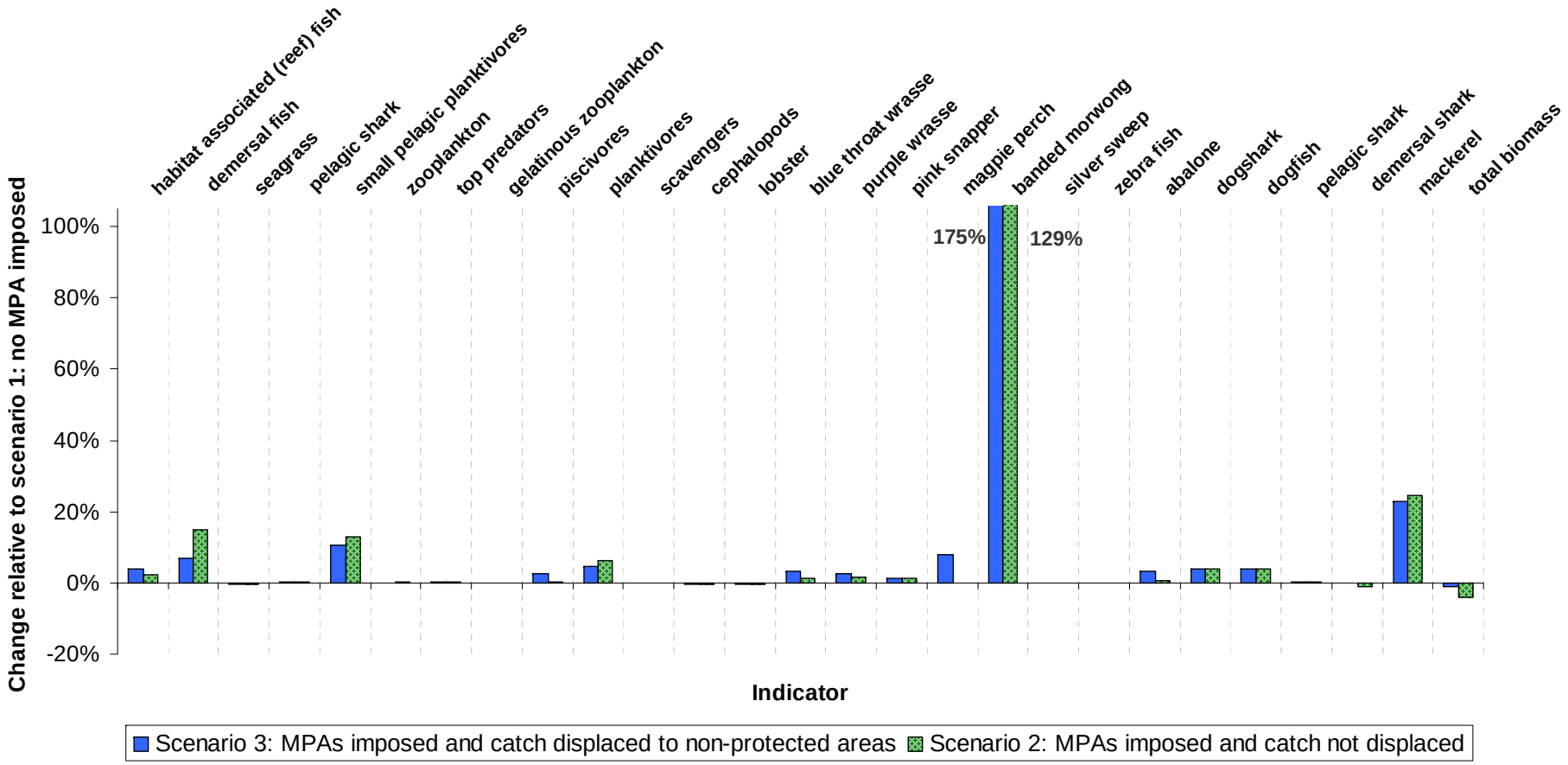

Figure 5-10: Difference in structural indicators between inside and outside the MPAs for scenario 2 and 3 relative to scenario 1

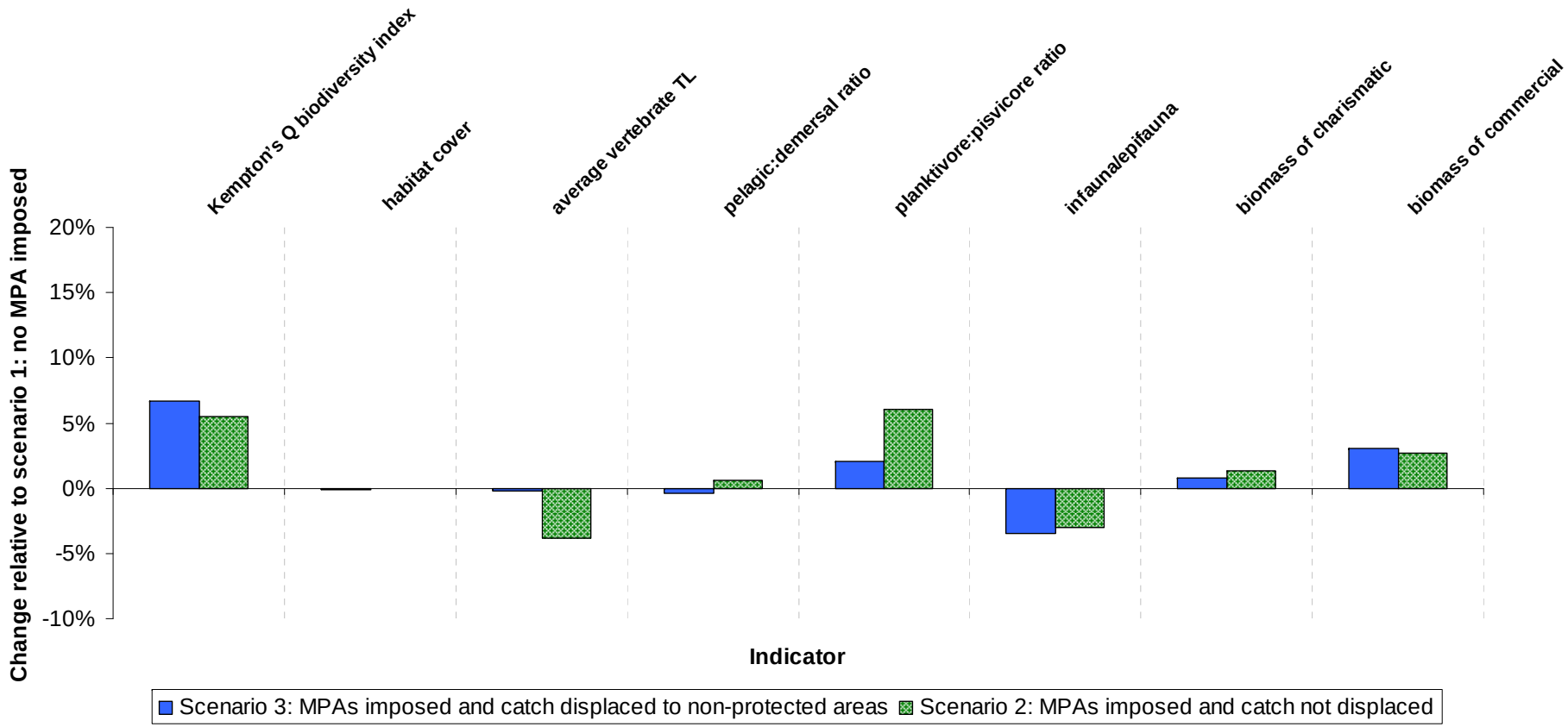

Figure 5-11: Difference in structural indicators between inside and outside the MPAs for scenario 2 and 3 relative to scenario 1

The indicators that differ most strongly between scenario 2 and 3, in terms of the difference between inside and outside of the protected areas, are: total piscivores, magpie perch, abalone and average trophic level of the system. The first three of these indicators see an increase inside the MPA compared to outside only in scenario 3, with no difference between the two areas in scenario 2. Average trophic level shows the opposite pattern, with a difference seen in scenario 2 (where the average trophic level decreases inside the MPA), but no difference seen in scenario 3.

Discussion

These results suggest that both conservation benefits and fisheries benefits are variable within a marine protected area, and the differences seen between scenario 2 and 3 indicate that ecosystem impacts may be highly dependant on the management that occurs outside of the protected zone. This is in line with other work which indicates that although MPAs are a useful tool for fisheries management, they may not work in isolation and should therefore be complemented by other management techniques (Tetreault & Ambrose 2007, Brady & Waldo 2009, Eklof et al. 2009, Kaplan et al. 2010).

Empirical studies have found that MPAs can provide benefits to top predators, often leading to increasing abundance both within and outside of the protected areas (Fanshawe et al. 2003, Guidetti 2007). Increases in the biomass of predators both inside and outside of the protected areas is seen in the simulations presented here. In scenario 2 there is an increase in demersal sharks, while dogsharks increase in both

scenarios 2 and 3. Observational studies (Schmitz 2004, Block et al. 2011) often equate increases in predator biomass with biodiversity (and system-level conservation benefits), thus it is of note here that the increases in predator biomass in the simulations presented here corresponds with an overall increase in total biomass within the MPAs, but does not strictly correspond with an increase in biodiversity. Specifically, the increase in predator biomass is more pronounced in scenario 2, while the increase in biodiversity is less pronounced in this scenario than in scenario 3. This discrepancy may be caused by the increase in predation that is also seen in scenario 2, especially from the demersal shark group. Menge and Sutherland (1987) found that biodiversity may be decreased in situations with consistently high predation. This is in line with the *intermediate disturbance hypothesis* (Grime 1973*)*, which states that biodiversity decreases under both low or high disturbance or predation conditions. (Menge & Sutherland 1987). Consequently, while an increase in predators may be a significant conservation benefit of the introduction of MPAs, this may correspond with a limit in biodiversity within the protected area, at least in the short term. It must be noted however that Kempton's biodiversity index is only one way of measuring biodiversity, which is especially suited to ecosystem models where functional groups are used to represent the biological component of ecosystems. Alternative measures of biodiversity should be used in future work to check the true conservation implications of results like those presented here. Moreover, the link between predation pressure and biodiversity should also be tested using other methods of assessing biodiversity and through empirical studies.

This effect of predation on the performance of MPAs highlights the importance of indirect effects when assessing MPAs. Many MPA models represent much fewer

species (Gerber et al. 2003), and therefore cannot take into account indirect species interactions as a result of the introduction of MPAs. Other efforts using multispecies ecosystem models (Walters et al. 1999, Savina et al. 2009, Albouy et al. 2010) have found indirect effects play a large role in determining which species benefit and which do not when MPAs are imposed. The fact that some fished species in these simulations decrease in biomass when the MPAs are introduced, even when there was no displacement of fishing effort (notably banded morwong, demersal fish and purple wrasse), shows that indirect effects may produce counter-intuitive responses within the system. Indeed, this phenomena has been observed in empirical studies, for example decreases in prey species such as abalone and urchins have been observed in Tasmanian MPAs during the first decade of their introduction (Barrett et al. 2007).

In addition to trophic cascades and indirect effects, the mobility of specific groups has also been shown to have a impact on whether these groups are protected by MPAs (Botsford et al. 2009). It has generally been found that groups with high mobility will not be as protected by an MPA as groups with very low mobility (Edgar & Barrett 1999, Walters et al. 1999, Murawski et al. 2000, Gerber et al. 2003). It is therefore imperative that both the representation of movement and an explicit spatial structure be included in model that are used to assess of the effectiveness of an MPA. While both juvenile and adult fish movement is handled explicitly in ASM, larval dispersal is presented in a much more rudimentary fashion. While this means that the results presented here must be treated with some caution, previous studies have found that the movement of adult fish can have a more pronounced impact on yields outside the MPA than does larval movement (Le Quesne & Codling 2008). While most of the groups that showed an increase inside the MPAs were relatively sedentary, the

increase in biomass of some of the more mobile species – notably the mackerel and small pelagics fishes – is counter to the idea that more mobile species will see less benefit from the MPA. There are two factors that are at play that cause this discrepancy. The first may be due to the size of the closures in the work presented here. While small to medium sized coastal closures (as seen in most real world examples) may not allow significant protection for mobile species, the very large closures that were used for this work provide a lot more protection for a larger proportion of the population, and therefore we are able to see differences in the response of highly mobile species that we otherwise would not. This increase then translates to increased biomass outside of the protected area, due to the mobile nature of the species. In other simulations with a much smaller closed area (not presented here), no increase in biomass was seen inside the MPA for mackerel, and therefore no spill-over effect was possible. The second cause of the increase seen in these mobile species is related to the spatial structure of the model. By using the telescoped model domain, the ASM model incorporates multiple smaller boxes inside the protected area (i.e. there are boxes that are entirely contained within the protected area, with all sides adjacent to other protected boxes). This has the effect of creating an area of protection for moderately mobile groups that is not easily provided for in less spatially complex models.

The ‘spill-over effect’ is one benefit that is suggested as an outcome to fisheries of implementing MPAs. This is where target species reach carrying capacity within the reserve and then excess individuals move into adjacent waters where they can then be caught by fishers (Kellner et al. 2007). In order for this phenomenon to take place the MPA must be effective in protecting commercial species to the extent that they can

substantially increase in biomass inside the protected area. The small increases seen in the biomass of banded morwong, abalone, dog shark and mackerel outside of the MPAs in scenario 3 (where fishing was displaced to the non-protected areas) shows some level of spill over for these species in this model. However, it must be remembered that the MPAs represented in these simulations were very large, so the results seen here are not necessarily in line with what might be observed around smaller scale closures of the size typically implemented.

Caveats

Models are caricatures of a system and so often omit processes or mechanisms found in the real world. For instance, two aspects of movement that may impact the performance of MPAs are not represented in these simulations. As mentioned above, the version of the Atlantis model used here does not represent larval movement, rather new recruits only appear in the system as they settle out of their planktonic stage. For the organisms with pelagic larvae, the planktonic stage is assumed to lead to a widespread distribution, and this is represented by a predetermined, fixed distribution of new recruits to the system. This means that a change in abundance of adults in one location may not lead to a similar change in abundance of new recruits in that location. In runs done with no dispersal of recruits, that is all new age classes recruited to the same location as their parents (not presented here) there was a quantitative change in the results (the difference between the two runs were more pronounced), but there was no qualitative change (the same groups were impacted in the same direction as the results presented here).

Similarly, movement of fishers is not represented at all in the work documented here, rather an averaged F is imposed across all non-protected areas. Consequently, their dynamic responses have not been considered; no economic model has been used to allocate fishing practises, or to regulate fish prices. Consequently, the variation in cost of fishing between the scenarios has not been examined, nor the time or effort required to obtain the yields discussed. These factors may impact the actual effects of an MPAs in a real world situation (White et al. 2008). Therefore, again, these results must be taken as indicative only and are not predictive of real outcomes. More detailed representation of both fishers and larval movement may improve the assessment capacity of this model. However, complex representation and parameterisation of both of these forms of movement would add further uncertainty to the output of the model. There is therefore a benefit in maintaining the simplified version presented here, which allows a clearer understanding of how fish movement and dispersal influences the performance of MPAs.

Conclusions

The results presented here support the notion that MPAs protect ecosystem health to some degree inside the protected area, and that very large MPAs may be effective to some degree in producing some 'spill-over' of fish yield to the surrounding areas. However, with the additional pressure that must be applied outside the protected area to maintain yields, the status of the overall system is not necessarily significantly improved by the introduction of MPAs. There are trade-offs between various objectives of MPAs that must be considered. In particular, protection of species of high conservation concern, especially predators, may have cascading effects throughout the food web, which may result in a loss of biodiversity, or at least

changes to the trophic structure of the ecosystem. In order to adequately capture complex system dynamics when modelling MPAs it is therefore important to represent multiple species as well as spatially complex model domains to allow for realistic movement of fish and invertebrates. The spatial parameterisation of the ASM model presents an innovative way to tackle spatial representation in ecosystem models and goes some way to addressing how these issues can be addressed when assessing the full implications of the introduction of MPAs.

Chapter 6. General Discussion

Using ecosystem models to inform ecosystem-based fisheries management

Fishing lower trophic level species

One of the most important contributions that ecosystem models can make to ecological understanding is highlighting the causes (processes or aspects of the ecosystem) that lead to particular dynamics. While the specific predictive ability of any particular model may have its limitations, by exploring how different scenarios or parameterisations play out, we can gain an insight into why particular outcomes are realised. For example, in the case of increased fishing pressure on lower trophic level species, the modelling in this thesis demonstrates that, although results between models were quite variable, consistent properties exist. These are that larger trophic impacts occur with the removal of species that comprise a larger fraction of the ecosystem's consumer biomass and are highly connected across trophic levels. This is critical information that can serve as the basis for further empirical investigations to determine whether these findings are consistent across systems and to show how important specific lower trophic level species are in a variety of marine ecosystem types.

Another role of models is to identify gaps in understanding and to raise new topics for investigation, which was the case in the earlier stages of this work. Although the investigation of fishing on lower trophic levels initially focused on fishing on squid populations in south-eastern Australia, during the course of the investigation it

became apparent that the impact of a depletion of myctophids could have a larger ecosystem impact than that of squid. Before this work was undertaken, the significant role of mesopelagic fish off SE Australia had not been raised. While there has been increased work done on understanding the distribution and abundance of myctophid fish over the past decade in this region (Olivar & Beckley 1994, Neira et al. 2000, Muhling et al. 2007), their role within the wider ecosystem had not been considered. Even though it has been suggested that mesopelagics play an important role as prey for commercially important species in some systems (eg New Zealand, (McClatchie & Dunford 2003)), to date, empirical research has primarily focused on quantifying their biomass.

The use of ecosystem models, and the findings discussed in chapter 4, has seen this issue more thoroughly explored. The research that forms the basis of chapter 4 has since widened to consider the impacts of the removal of a range of lower trophic level species across a wider range of models and systems (Smith et al. 2011), where similar results have been found. The significance of mesopelagics is now being recognised by national fisheries management (e.g. these species are being considered explicitly in vulnerability analyses). Internationally the role of lower trophic levels is being recognised in ecosystem based fisheries management (EBFM) guidelines by bodies such as the Marine Stewardship Council (MSC) (http://www.msc.org/ accessed August 2011). The MSC technical advisory board has recommended that new guidance be provided relating to the specific assessment requirements of lower trophic level species, specifically the report states:

> "A generic target reference point (TRP) for a key lower trophic level (LTL) species shall be substantially higher than the TRP determined … in a single species context, and in any case it shall not be less than 40%B_0….
>
> The default target reference point shall be 75% of the spawning stock level that would be expected in the absence of fishing, i.e. 75%B_0.
>
> b. Lower target reference points between 75%B_0 and 40%B_0 may still achieve 80 level scores if it can be demonstrated, through use of published trophic models for the fishery/ecosystem being assessed (such as Atlantis or Ecosim) that the level adopted does not:
>
> i. lead to the abundance levels of more than 15% of the other trophic groups being impacted (i.e. altered from their state in the absence of fishing on the target LTL species) by more than 40%; or
> ii. lead to the abundance levels of any other group being impacted by more than 60%." (http://www.msc.org/about-us/consultations/current-consultations/assessment-of-low-trophic-level-fisheries/consultation-document-draft-tab-directive-ltf)

Using spatial management to apply EBFM

While defining acceptable levels of depletion is one aspect of EBFM, spatial management is another and insights on its use can also be gained using ecosystem models. While the work done on spatial management in this thesis has not had as far reaching implications to date as that on the lower trophic level species, the information provided in chapter 5 contributes significantly to the topical discussion of the effectiveness of MPAs for protecting biodiversity and ecosystem structure and function. The MPA-biodiversity finding of chapter 5 puts into question some of the assumptions about the conservation benefits of MPAs. Although there are a great

many examples of where MPAs have increased the biomass of particular species (eg, lobsters in Tasmania (Edgar et al. 2009), mud crabs in Moreton Bay Marine Park (Pillans et al. 2003), coral trout, red emperor and redthroat emperor in the Great Barrier Reef Marine Park (McCook et al. 2010) the claim that MPAs universally increase biodiversity is not well supported empirically to date. Research such as that presented in chapter 5 goes some way to demonstrating that, although there may be increases in abundance of some groups with the imposition of an MPA, this does not necessarily lead to the increase in overall biodiversity – particularly if additional off site management is not employed. As not all systems will respond in the same way to particular management actions (Hilborn & Litzinger 2009), tools (including ecosystem models) allowing for an evaluation of drivers, processes and potential outcomes are essential for providing effective guidance to management.

Insights gained from the work in this thesis into the appropriate uses of ecosystem models

Continued model development and multiple uses

Complex ecosystem models work best when they undergo iterative improvement, based on a commitment by ecologists to produce a model capable of capturing system dynamics (Logan 1994). Rarely will the first parameterisation of a model such as Atlantis be the most accurate representation of a system, and only through ongoing use and modification can we ensure model refinement. As such, they are often under constant revision, either to amend discrepancies with observations by incorporating new process understanding, or by updating with new data or system shifts. The models described in this thesis are no exception. Both the SETas and ASM models

were implemented during the course of the research outlined in the previous chapters. Since then both the models have been refined. The ASM model in particular, has received substantially more attention (Smith et al. 2010) so that it is more responsive to system perturbations, has an improved fit to observational data and is being expanded to include processes pertinent to climate change mechanisms. Although the results of this refined version do not vary substantially qualitatively, there are some quantitative changes in response to perturbations and variations in management. It is important to keep the possibility of upgrades and model revisions in mind when analysing model simulation output, as there is always the potential for changes in model structure or calibration to lead to changes in output.

All ecosystem models are complex and time consuming to create and interpret. For example, the creation of the ASM model took nearly 3 years before it was at a stage that could be used to explore simulations. The development of these models therefore cannot be undertaken lightly or without the potential for additional future uses.

Using alternative model parameterisations

An important lesson learned from this work is that the parameterisation of the system state has significant consequences for the outcomes of model experiments. Various parameterisations of the same model can be made. For example, the choices made in parameterisation can lead to: highly stable, or highly unstable systems; groups with mainly generalised diets, or with highly specialised diets; or systems with high production and high consumption by predators (top down control), or low production and a bottom up controlled system. All these aspects will influence how an ecosystem model will respond to perturbations, and therefore what conclusions are drawn from

the model output. Pinnegar et. al (2005) for example, demonstrated that models with highly aggregated lower trophic groups show a higher degree of resilience to system perturbations than models that represent these groups more explicitly. This, they suggest, may mean that if one is not careful, then the psychology of the scientist constructing the model could affect the model behaviour and predictions.

This is an important issue, as the parameterisation of complex ecosystem models can be highly uncertain, due to the lack of sufficient data with which to populate the model. While some biological, hydrodynamic and social aspects are well documented and understood, many marine ecosystem dynamics are not. For example, while stomach contents analysis provides important information on the major prey items for a certain species, it is less likely to pick up minor prey species, or prey that is only taken when there is little else available. However, these minor prey items can hold a key place in phase transitions between alternative system states, therefore capturing them effectively in ecosystem model parameterisations is important. Similarly, scope for shifts in predatory behaviour must be included, as such changes may occur with climate change or species depletion, simply because of the opportunistic nature of many fish (i.e. a predator may not consume much of a particular prey if it has little exposure to that prey item, but under changed dynamics prey abundance and accessibility may increase seeing it become a key dietary item). The differences in the predictions of the two versions of the AMS model in chapter 4 highlight how changes in dietary parameterisation can influence model output. This issue highlights the importance of empirical data as model input and for model validation.

The comparison of various model structures that contain a variety of realistic parameter sets that was performed in chapter 4 is one way to test the robustness of results. While this does not guarantee that the model predictions are 'accurate' it provides insights into which factors are important in controlling particular system dynamics. The value of the ecosystem model lies in its ability to highlight the characteristics that define a commodity of interest. For example, while it is difficult to say with confidence that myctophids are a keystone species in south-eastern Tasmania (as suggested in chapter 2), the work in chapter 4 builds on that initial work and allows us to conclude with greater confidence that a species with high abundance and a high degree of connectivity with other species in the system has the potential to play a keystone role in that system. That summation can then be used to direct empirical research to identify or confirm potential keystone species.

Handling data limitations and knowledge gaps

Many of the weaknesses of ecosystem models are related to their large, complicated and complex nature, which calls for extensive and often long term data sets. The large data demands can often be hard to fill, and therefore data from other locations or taxonomic groups may be the only way to parameterise a model. Such an approach however, must be used with caution, particularly when choices must be made between conflicting, but apparently similarly appropriate, parameter values. The more uncertainty in the input data used, the more uncertain the model outputs (Ludwig & Walters 1981). This is especially the case with highly complex models that incorporate feedback loops and high degrees of interaction between the various components.

Ludwig & Walters (1985) suggest that the complexity of a model must be governed by the amount of information available, and if there is a lack of reliable data, a simple model is preferable. While simple models are appropriate in some instances, such as for very data poor areas (Ludwig & Walters 1981, Ludwig & Walters 1985, Hurtt & Armstrong 1996), oversimplification can lead to a model that does not reflect reality in any practical way (Logan 1994). Therefore, an optimal level of complexity, that minimises computational and data requirements, but still provides robust predictions is required. The telescoping technique provides a way to manage spatial complexity to both maximise accuracy and minimise uncertainty. This approach can be applied to a wide range of ecosystem modelling projects where the detail of available data varies spatially within the area of interest.

Limitations of ecosystem models

Model assessment and the predictive power of ecosystem models

It has been argued that complex ecosystem models lack accurate predictive power (Berryman 1991). Another way to approach this however is to acknowledge that many ecological dynamics display inherently chaotic properties, which makes them unpredictable in a specific sense (Logan 1994), even if their general dynamics can be captured faithfully. Therefore it is pertinent to reassess whether specific prediction is a reasonable goal in ecology. Given the increasing list of general system features being discovered empirically and through theoretical tools like models, and the "unreasonable effectiveness of mathematics" (Wigner 1960), it is important to ask whether we should limit our research to trying to understand system dynamics so that

we can gain some grasp of the range and quality of the types of changes that we can expect under perturbations, rather than trying to quantify exact changes.

There may be arguments around specific prediction and empirical ecology, but a much more extensive discussion exists in the theoretical literature. For instance, Schnute and Richards (2000) provide an interesting discussion of the limitations of mathematical models when applied to fisheries management. They raise the important point that while mathematical models can be used with confidence in the physical sciences, biological sciences do not have such a high level of certainty on which to ground their models. Indeed, ecology as a science depends on statistical analysis of data, which implies an essential degree of uncertainty. It is important to recognise that complex ecosystem models are not intended to be used as predictors of specific ecosystem function. Rather, their use lies in providing general trends and insights into *potential* ecosystem responses to various pressures that may be applied either anthropogenically or otherwise.

Model Uncertainty

A major criticism of ecosystem models is their inability to quantify uncertainty by applying definitive confidence boundaries to the output in the way that single species (or simpler multispecies) models do. Indeed, the highly complicated nature of the models make a traditional sensitivity parametric analysis impossible. One technique used to partially overcome this is to ‘bound’ the output by running simulations with a range of ecosystem states, from highly productive, to low levels of productivity. This treatment of uncertainty is neither extensive nor exhaustive, however it is a rudimentary method for dealing with uncertainty in model output. This approach has

been shown to be a useful method in other studies (e.g. Fulton et al. (2007)). It does however, depend on the assumption that alternative parameterisations lying between the bounding sets do not produce dynamic results that are beyond the outputs provided by the bounding parameter sets. The parameterisation of these bounding states therefore requires care and takes extensive user expertise, or expert input, into the possible states of the system. Furthermore, this bounding cannot take into account unknown feedback loops – or indeed any other "unknown unknowns" (Rumsfeld 2002). Thus, although this approach is a move towards containing the uncertainty in ecosystem models, it must be acknowledged that there is a level of heuristic subjectivity in the interpretation of these models and their confidence bounds.

Model transparency

In current uses of ecosystem models there can be a lack of transparency that inhibits ease of pick up by other researchers – results are replicable, but not without significant effort (potentially many years), investment of resources and training. This is made more difficult by the vast number of parameters, the heuristic form of calibration that is still used with many models and the difficulty of reproducing these in a standard scientific publication. This leaves models and model users open to accusations of non-objectivity (Logan 1994). This is an issue that need to be born in mind when working with ecosystem models, and more work needs to be done to find ways around them. For instance, by making a model publicly available for independent use, it reduces the issues of non-transparency[3]. Furthermore, creating websites where full details of model parameterisations (that cannot feasibly be

[3] While Atlantis is available for public use, the lack of user friendliness and documentation in it's current state makes independent usage without extensive support extremely difficult.

included in scientific publications) can be stored and publicly accessed would allow other researches to not only see the model formulation and structure, but also to replicate results, or investigate how small changes might change the results. Although this would not currently be an easy undertaking for anyone without experience with Atlantis, over time, with more users and more documentation and user friendliness incorporated into the modelling framework, it would greatly improve the level of scientific scrutiny and therefore the rigour - and the perception of rigour - of the modelling process.

Conclusions

There is a great scope for ecosystem models to bring to light dynamics that may not have been questioned or supposed to exist previously. This has been the case throughout the development and testing of the models presented in this thesis. Although the criticisms of complex ecosystem models are relevant if the model is to be used directly to determine management actions, they become less of a problem if the model is to be used as a guide to demonstrate *possible* impacts of alternative management strategies (Fulton et al. 2003). Large, complex models are a way to perform 'experiments' that otherwise cannot be done in the real world. Indeed, empirical experiments often involve the same type of trade-off between realism and comprehensibility, as is seen in the trade-off between complex and simple models. That is, large ecosystem level experiments produce results that are complex and difficult to interpret, and small scale laboratory experiments are more controlled and understandable, however they may not represent the realities of the world outside the lab (Van Nes & Scheffer 2005).

Complex ecosystem models are in the early stages of development – this thesis explores the use of the Atlantis ecosystem model, and contributes to the discussion of appropriate techniques that can be used for ecosystem modelling. While ecosystem models cannot and should not be used as absolute predictors of ecosystem dynamics under perturbed systems, they can be useful to inform qualitative impacts that may arise from various ecosystem impacts and uses.

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